THE
AMERICAN NATURALIST

VOL. LV. *March–April, 1921* No. 637

IMMUNE SERA AND CERTAIN BIOLOGICAL PROBLEMS[1]

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Mr. President, Members of the Academy of Medicine of Cincinnati: I am deeply appreciative of the honor conferred upon me by the invitation to address this medical society. Although my own researches have lain outside the conventional limits of medicine, it happens that several of them have crossed the border lines of this science and have thereby quickened the naturally keen interest in the scientific aspects of medicine that I have always entertained. In my present researches, indeed, I have borrowed some of my most important tools and ideas from the field of immunological studies and discoveries, made in the main by medical researchers. The luxuriant growth of literature in recent years on immunity, antitoxins, cytotoxins, bacteriolysins, hemolysins, opsonins, precipitins, agglutinins, anaphylaxis, and what not, is known to you all. Naturally, the brilliant series of practical applications of this new knowledge in diagnosis, prophylaxis and therapeutics, stimulated every medical investigator to redoubled effort until the field has become almost exclusively the domain of the bacteriologist and the pathologist.

It may seem presumptuous of me, a biologist, to step outside the traditional bounds of my science and to come, carrying coals to Newcastle as it were, in recounting to you various facts long since learned by physicians—

[1] An address delivered before the Academy of Medicine of Cincinnati.

facts which lie at the very foundation of modern medical theory and practice. I offer my apology in advance for the lack of novelty in much of what I shall say. My only justification is that a reconsideration of such familiar knowledge gives one a good running start, so to speak, for a leap into less known realms; realms of great interest to the embryologist, the cytologist, the student of heredity and of evolution; regions in which lie hidden the secrets of all life and form, of hereditary transmission, and of its converse, variation.

It is clear that the phenomena which constitute the field of immunology, although to-day viewed mainly from the standpoint of infection and immunity, all have broader biological aspects. They must in last analysis be but heightened or specialized reactions of the fundamental processes which underlie all life phenomena. They are but one of the many expressions of that delicately balanced stereochemical system we call protoplasm, and they are inextricably interwoven in the ebb and flow of metabolism, with such fundamental biologic processes as growth, reproduction, irritability and adaptation.

The physiologically minded biologist also inevitably suspects close relationship between the reactions described by the serologist and those manifested normally in a living animal by that wonderful system of chemical messengers or internal secretions, the hormones and chalones, which, independently of the nervous reflex, can stimulate or inhibit the activity of some organ in a part of the body far distant from the source of the secretion itself, and which undoubtedly play an important part in development. There seems no reason to doubt that both hormones and antibodies, for example, represent complexes of atoms which were originally parts of body-cells concerned in the normal metabolic processes. One is extruded into the body fluids under the influence of a usual and therefore normal stimulus, the other is the product of an accidental stimulus resulting from disease or other unusual condition.

In any event this whole field of endocrinology and serology stands as a perpetual challenge to the experimental biologist. Some sixteen years ago Nuttall published his remarkable series of studies on "Blood Immunity and Blood Relationship" in which he reported the results of his examination of some nine hundred different samples of blood from various kinds of animals. He demonstrated that by the precipitin test a differential scale of actual blood relationships among animals can be established. As you doubtless recall, when an animal of one species is injected parenterally with successive doses of blood-serum of another species over a period of a few weeks, the blood-serum of the injected animal acquires the ability to form a precipitate with that of the alien species when the two sera are mixed. When the reaction is carried on in vitro, even in dilute solutions, the cloudiness and ultimate flocculation which results are easily seen. If, for example, a rabbit is thus repeatedly injected with human blood its blood-serum when mixed with slightly diluted human blood-serum in vitro will almost instantly yield a noticeable precipitate, though a control mixture of human blood-serum and the blood-serum of an untreated rabbit will remain clear. The ingredient which has been engendered in the serum of the rabbit is termed a *precipitin,* and the foreign serum which was injected—human blood-serum in this case—is called the *antigen,* or more specifically, the *precipitinogen.* It is known that not only blood-serum, but also milk, globulins, various albumins and bacterial products—in fact probably any foreign protein—may serve as antigen for the formation of precipitins. The reaction is not absolutely specific in low dilutions since species of animals related to the one from which the antigen was taken will also, though in less degree, give the effect. Closeness of relationship is determined by finding the dilution in which the serum to be tested will react. For instance, Nuttall found that when rabbit serum which has been sensitized against human serum is mixed with the moderately di-

luted sera of man, apes and monkeys, respectively, it reacts to all, though in a varying degree. When mixed with more highly diluted sera from such animals, it forms a precipitate only with the serum of man and the manlike apes (chimpanzee, orang-outang, gorilla), the chimpanzee standing nearest to man. Absolute specificity may be obtained if the antigen is sufficiently diluted. On the basis of extensive experience, Uhlenhuth sets a dilution of antigen of 1 to 1,000 as a standard beyond which no precipitation will occur except with the specific antigen employed in the sensitization.

Thus the precipitin test became useful to the zoologist in discriminating between different species, and it may prove of importance in establishing the taxonomic position of new forms, or in confirming or changing the classification of groups already known. The delicacy of the test is remarkable. A properly sensitized serum may give a reaction with blood diluted 20,000 or even 50,000 times. Sera have been obtained, indeed, in which specific antigen could be detected in a dilution of 100,000. When one recalls that ordinary chemical tests cease to give detectable reactions in blood diluted 1,000 times, he can appreciate the value of these physiological methods of measurement to the biologist. They apprise him of species differences between the proteins of various animals which can not be determined by any known chemical methods.

The value of the precipitin test in forensic medicine, in determining the nature of blood stains on clothing, weapons or other objects, is well known to all of you, as is doubtless their utilization in meat inspection, such as for the detection of horse-flesh or dog-flesh in sausages or other chopped meats, and in various other types of adulteration.

One thing that interests the biologists greatly in the precipitin reactions is the fact of so-called "species specificity"—the fact that blood sensitized against one tissue of a given foreign species will react with extracts of

the other tissues of that species. Thus the blood-serum of a rabbit which has been treated with sheep blood-serum will form a precipitate not only with the sheep serum, but with the extracts of sheep muscle, sheep liver, sheep spleen, and other organs of the sheep. This clearly implies that each species of animal possesses something in common throughout all its tissue proteins, something peculiar to that particular species which in last analysis must be resolved into a problem of its general metabolism and stereochemistry. This does not mean that organs may not also have protein complexes peculiar to themselves. Indeed, it is an established fact that they do. And what is more, some of these organal peculiarities may be common to various species. For example, the fact of "organ specificity" has been established for the crystalline lens. According to Uhlenhuth, immunization with crystalline lens of a given species of animal yields a precipitin which reacts with the lens proteins of many different species of animals. Von Dungern and others have secured similar results with proteins derived from the testis. Confirmatory evidence of this fact that a type of specificity attaches to the nature of the organ itself, irrespective of species, has also been established by means of the reaction of anaphylaxis.

The precipitin reactions, then, teach the biologist that in the chemistry of the general proteins of a given animal, there are certain fundamental similarities, also that there are constant species differences between the homologous proteins of different species of animals, and lastly, that some proteins, in certain highly specialized organs at least, though existing in different species, possess similar chemical characteristics.

These and related facts when considered in conjunction with such as those of Reichert and Brown regarding the stereochemical correspondences in the living matter of allied species as demonstrated in the crystallography of their hemoglobins, or the studies of Reichert on the relations of the starches and tissues of parent-stocks to those

of hybrid-stocks in plants—such facts taken all together are gradually constructing for the biologist a rational biochemic basis for the study of the fundamental processes operative in metabolism, heredity and evolution.

But let us now turn our attention to another type of serological reactions, those concerned with the cytotoxins or cytolysins. You doubtless all recall the well-known experiments of Bordet, in 1898, in which he found that the blood of guinea-pigs which have been repeatedly injected with the red blood corpuscles of the rabbit, acquire the property of rapidly dissolving rabbit corpuscles. This is the familiar phenomenon of *hemolysis,* and the substance in the blood-serum of the guinea-pig which brings about solution of the red corpuscles of the rabbit is termed a *hemolysin.* Bordet showed further that this enhanced solvent action of the serum of animals treated with the red blood cells of a different species exists only for the kind of red corpuscles used as antigen, not for those of other species of animals. Exceptions occur, though in the main the reaction is specific. The similar facts regarding bacteriolysins, which are now commonplaces of every-day medicine, had been established a year earlier.

It was soon discovered that other materials such as leucocytes, nervous tissue, spermatozoa and crystalline lens, when injected into the blood of a foreign species will form lytic or toxic substances more or less specific for the antigen used in the immunizing process. While it is probable that none of such cytotoxins or cytolysins acts only upon its own antigen—all studied so far have been found to be somewhat hemolytic—the important fact, for our present purposes, is that although a particular cytolytic serum may affect some other tissues, it vigorously attacks the special tissue used as antigen.

This fact, when fully grasped, suggests inevitably to the biologist, or at least to the investigator interested in the mechanism of heredity and variation, queries such as the following: if a special serum can thus be constructed

which will single out and destroy a certain element of an adult organism, is it not possible that there is sufficient constitutional identity between the mature substance of that element and its representatives in the germ-cell that they too will be influenced? Is this not a way of getting at the old yet ever new problem of the inheritance of body acquirements, or at least of breaking in on the germ? Is it not possible to secure selective action on certain parts of the developing embryo and thus shed some light on the genesis of congenital abnormalities? And by using the cytolytic and other immunologic methods may not additional knowledge be gained concerning the relations of mother and fetus?

Of this series of problems the one which tantalizes the biologist most of all, perhaps, is that concerned with the possible hereditary transmission of characters acquired directly by the body of a parent. As you know, this has been a bone of contention for many years. The so-called Neo-Lamarckians follow, at least in a modified form, the teachings of Lamarck to the effect that such "acquired characters" are or may be inherited; the other school, often called Neo-Darwinians, strenuously deny such inheritance, and assert that the sole font of specific change lies in the germplasm. According to them any new inheritable feature which appears first arises in the germ and only finds somatic expression when this germ develops into a body.

How important he considered the correct solution of this problem is shown in the following statement of Herbert Spencer. He said: "Concerning the width and depth of the effects which the acceptance or non-acceptance of one or the other of these hypotheses must have on our views of life, the question, Which of them is true? demands beyond all other questions whatever the attention of scientific men. A grave responsibility rests on biologists in respect of the general question, since wrong answers lead, among other effects, to wrong belief about social affairs and to disastrous social actions."

Lamarckism at the present time, among American biologists, has all but disappeared. Some palæontologists, who in reading the records of the past find that whenever new conditions for existence occurred, new forms of life admirably adapted to those conditions appeared, are prone to believe that the environment has in some way directly molded these new inhabitants to its bounds. Since this performance has occurred again and again, they are a bit skeptical of the selectionist tenant that each occasion has had to await, not only the accidental occurrence of a favorable germinal variation, but of a host of them, which must in turn be sifted and parceled and perfected by natural selection into that adaptedness to the surroundings which characterized the organisms in question. Various students of geographical distribution also are inclined to regard the direct action of environment as instrumental in molding the fauna of a given region. In brief, those who look at the problems of evolution from wide perspective tend to postulate that altered function or environment, if long continued, in some way modifies descendants, but they don't tell us how. Those who view the problem from the standpoint of the few generations intensively studied by the geneticist, or from the germ-cell lineages of the embryologist, or the chromosomes of the cytologist, almost without exception reject the Lamarckian interpretation. And it can not be denied that the latter have an incomparable advantage in directly testing the matter, since they have their material in hand for direct observation or experimental control. So it has come about that the believer in Lamarckism, silenced if not convinced by the formidable array of negative evidence amassed against him, and still more perhaps by his own inability, from the basis of carefully controlled experiments, to cite specific examples of inherited somatic acquirements, has subsided into mute acquiescence or but faint-hearted advocacy of his theory.

The fertilized egg develops into an adult individual

through a series of cell-divisions and specializations of the new cells thus produced. During development certain cells are set apart, often very early in embryogeny, for reproducing the next generation. Thus the germ-cells and the body-cells of a given organism develop at the same time and neither is the product of the other; each alike has originated by division from the fertilized ovum. There is no necessity, therefore, for collecting samples from all parts of the body and concentrating them in germ-cells, as Darwin supposed was done, for the samples are already there, derived from the same supply that produced the parental body. They exist not in the form of such parts of an organism as are visible to us, but simply as certain ingredients which when combined in certain ways and developed in certain directions give rise to the parts in question. Sooner or later the body dies, but in the meantime one or more of the germ-cells have passed on to become expressed as new bodies and new germs. Thus a child does not inherit its characteristics from corresponding characters in the parent-body, but parent and child are alike because they are products of the same fundamental materials.

How, indeed, can a change in a brain-cell or a muscle-cell find expression in a germ which is itself a cell that possesses neither brain nor muscle? How can an influence at a distant part of the body even reach a germ-cell? How can immature young, even larvæ in some instances, produce young which ultimately come to manifest the characteristics of the adults of the species? How can recessive Mendelian unit-characters disappear, perhaps for generations, to reappear at last apparently with qualities undimmed? How, on the Lamarckian basis of use-inheritance, can the highly specialized characters of the worker-bee have originated and become perfected when the individual itself is sterile? How account for adaptive characters based on passivity, or for mutual adaptations such as may exist between plants and certain animals? These and a host of questions like them con-

front the Lamarckian when he strives to resuscitate the faith that is in him.

The opponent of Lamarckism certainly shines as a disconcerting questioner. Moreover, he is clearly correct in his contention that the idea of germinal continuity is the simpler one, and probably the only tenable one, as regards the inheritance of characters, *once they have been engendered.* But the crux of the whole problem lies in the question, where do new characters come from? According to the followers of the great biological theorist, Weismann, not only do new heritable characters originate in the germ, but a change which first appears in the body can not in any way become incorporated in the germplasm. Unquestionably, constitutional changes in a germ-cell at any time may find expression as a new or modified character in the subsequent organism which comes from this germ. But while this is an obvious fact, it gives no real explanation of the origin of the character in question, since it tells us nothing about what induced the constitutional change. Weismann regarded sexual reproduction, the intermingling of two lines of germplasm, as an important cause of germinal variation, but our modern genetical studies indicate that this is probably not true. Dual ancestry, of course, makes possible new arrangements of germinal constituents which reveal themselves in new combinations of characters, but the germinal antecedents of such combinations are unitary in nature, and there is no evidence that sexual mixture originates any new units. So the Neo-Darwinian, although highly successful in pointing out the shortcomings of Lamarck, has been little if any more successful in explaining satisfactorily how changes are *initiated* in the germ-cell. Yet it is this very item of change, of *variation,* that is the real basis of evolution.

Some selectionists glibly assert that new characters arise as the result of spontaneous changes in the germ. What is meant by this? Just what is a spontaneous change? No one has ever succeeded in telling us. And

we may suspect, though perhaps it is heresy to do so, that it is a well-sounding phrase that is the equivalent of the three words, I don't know. Unwilling to admit of the modifying influence of external agencies on the germ, such theorists resort to the fiction of a spontaneous change. Coleridge somewhere has said "What's gray with age becomes religion." We have toyed so long with this idea of germinal continuity and the invulnerability of the germ, that it has become for some of us well nigh sacrosanct. Living matter is living matter wherever it may be found, but when it happens to be in the germ-cells, verily, "this corruptible has put on incorruption and this mortal immortality"!

Now, no one to-day, qualified by his knowledge of embryology and genetics to the right of an opinion, would, I think, deny that the new organism is in the main the expression of what was in the germ-line, rather than of what it got directly from the body of its parents, but does this fact necessarily carry with it the implication that the germ is insusceptible to modification from without? Is not the serum of organisms with blood or lymph an excellent medium through which external influences may operate upon it? Is it not more reasonable to postulate the origination of germinal changes through some such mechanism as this than to attribute it to mysterious "spontaneous changes"?

With such thoughts in mind I and my research associate, Dr. E. A. Smith, set about making various tests.[2] Without attempting to tell you of our as yet unsuccessful attempts to secure cytolysins which will operate in the developmental stages of such periodically renewed structures as feathers, or to weary you with the history of our various other failures—of which there are an abundance—I wish to speak briefly about certain antenatal effects we secured in rabbits by means of fowl-serum sensitized against rabbit crystalline lens, and of the fact that such induced defects may become heritable.

[2] *Jour. Exp. Zool.*, XXXI, 2, Aug., 1920.

The crystalline lens of the rabbit was selected as antigen, and fowls as the source of the antibodies. The lenses of newly killed rabbits were pulped thoroughly in a mortar and diluted with normal saline solution. About four cubic centimeters of this emulsion was then injected intraperitoneally or intravenously into each of several fowls. Four or five weekly treatments with such lens-emulsions were given. Then a week or ten days after the last injection the blood-serum of one or more of the fowls was used for injection into pregnant rabbits. The rabbits had been so bred as to have the young advanced to about the tenth day of pregnancy, since from the tenth to the thirteenth day seems to be a particularly important period in the development of the lens. It is then growing rapidly and becomes surrounded by a rich vascular network that later disappears. From four to seven cubic centimeters of the sensitized fowl-serum were injected intravenously into the pregnant rabbits at intervals of two or three days for from ten days to two weeks. Several rabbits died from the treatment and many young were killed in utero. Of sixty-one surviving young from mothers thus treated, four had one or both eyes conspicuously defective and five others had eyes which were clearly abnormal. It is possible that still others were more or less affected, since we judged only by obvious, visible effects. We found later in some of the descendants of these individuals that rabbits which passed for normal during their earlier months subsequently manifested traces of defects in their lenses or in other parts of the eye.

The commonest abnormality seen in both the original subjects and in their descendants was partial or complete opacity of the lens, usually accompanied by reduction in size. Other defects were cleft iris, persistent hyaloid artery, bluish or silvery color instead of the characteristic red of the albino eye, microphthalmia and even almost complete disappearance of the eyeball. Taking into account the method of embryological devel-

opment, however—the relation of lens, optic cup and choroid fissure—the defects are probably all attributable to the early injury of the lens. In some cases, both among originals and descendants, an eye microphthalmic at birth may undergo further degeneration such as collapse of the ball and what appears to be a resorption as if some solvent were operating upon it. The eyes of the mothers apparently remained unaffected. This is probably due to the fact that the lens tissue of the adult rabbit is largely avascular and therefore did not come into contact with the injected antibodies.

That the changes in the eyes of the fetuses resulted from the action of lens antibodies is indicated by the fact that in not one of the forty-eight controls obtained from mothers which had been treated with unsensitized fowl-serum or with fowl-serum sensitized to rabbit tissue other than lens, was there evidence of eye-defects, and I may add, that among the hundred or more young obtained later from mothers which were being experimented upon with various types of sera or protein extracts, for other purposes, not a single case of eye-defect has appeared.

As already stated, once the anomaly is secured it may be transmitted to subsequent generations through breeding. So far we have succeeded in passing it to the eighth generation without any other than the original treatment. The imperfection, indeed, tends to become worse in succeeding generations and also to occur in a proportionately greater number of young. Though not analyzed completely as to its exact mode of inheritance, it has in general the characteristics of a Mendelian recessive. Like such anomalies as brachydactyly or polydactyly in man, the transmission is not infrequently of an irregular, unilateral type, sometimes only the right, at others only the left eye showing the defect. In the later generations, probably in some measure as the result of selective breeding, there is an increasing number of young which have both eyes affected.

To determine whether the reappearance of the defect was due merely to the passing on of antibodies or kindred substances from the blood stream of the mother, or to true inheritance, we mated defective-eyed males to normal females from strains of rabbits unrelated to our defective-eyed stock. The first generations produced in this way were invariably normal-eyed, but when females of this generation were mated to defective-eyed males again, we secured defective-eyed young after the manner of an extracted Mendelian recessive. It is obvious that in such cases the abnormality could only have been conveyed through the germ-cells of the male, and that it is, therefore, an example of true inheritance. Subsequent matings have shown that these young transmit the eye-anomalies as effectively as do individuals of the original lines. A new strain of defective-eyed young, established about the time our original paper went to press, is also flourishing and, as regards transmission of the defect, seems to differ in no way from the earlier stock.

But now, let us inquire as to where all this leads. Without entering into a discussion of just what, serologically, is taking place in the body or in the germ of fetuses borne by the lens-treated mothers, the point I wish to emphasize is that a certain specific effect *has* been produced; and, what is of greater moment, once the condition is established it may be not merely transmitted, but inherited. Whether the lens of the uterine young is first changed and then in turn induces a change in the lens-producing antecedents in the germ-cells of these young, or whether the specific antibody simultaneously affects the eyes and the germ-cells of the young is not clear. In any event it is evident that there is some constitutional identity between the substance of the mature organ in question and the material antecedents of such an organ as it exists in the germ.

Biologically considered, the most significant fact is that specific antibodies can induce specific modifications in the germ-cell. Whether these antibodies are trans-

mitted from the mother's blood or engendered in that of the young would seem to be of secondary importance. It stands to reason that antibodies originated in an animal's own body will modify germinal factors if corresponding antibodies introduced from without can accomplish this.

The whole question as to how important such a fact may be in contributing to an understanding of the causes of the germinal changes in organisms in general, which lead to variation and evolution, hinges on the question of whether changes in an animal's tissues will induce the formation of antibodies or kindred active substances in its own body. We have steadily accumulating evidence that such reactions do occur.

In our own laboratory, for example, after many attempts we have succeeded in securing a defective-eyed young rabbit from a mother of normal stock by injecting her repeatedly with pulped rabbit lens before and during pregnancy. Since the young rabbit in question has both eyes badly affected there can be no question that a rabbit can build antibodies against rabbit-tissue which are as effective as those engendered in a foreign species such as the fowl. We have likewise found it relatively easy to secure spermatoxins by directly injecting rabbits, both male and female, with rabbit spermatozoa. Moreover, a given male will develop antibodies against his own spermatozoa if he is injected intravenously with the latter.

We are also securing evidence that serologic reactions induced in the fetus through operations on the mother are not mere passive transmissions, but may become actively participated in by the tissues of the fetus. For example, female rabbits sensitized with typhoid vaccine followed by living typhoid germs may transmit to their young and even to their grand descendants the ability to agglutinate typhoid bacilli in serum diluted from 60 to 160 times. From the standpoint of heredity we have no reason so far for maintaining that this is anything but

placental transmission, though we are going to practice immunization generation after generation for a number of generations to determine if a truly hereditary immunity will be established. However, facts have come to light which show that there is more concerned in the operation than a mere transfer of antibodies from mother to fetus. For instance, the blood of young shortly after birth may show a higher titer than that of the mother. Again, after two or three months of development the young of certain of the sensitized mothers have shown a rather sudden rise in titer, much above that of the mothers. In such cases it would seem that some mechanism in the young rabbit itself is constructing antibodies which supplement those passively derived from the mother. Possibly in the process of development some organ important in such reactions just came into functioning. If this is true further experiments may throw some light on the perplexing question of the source or sources of the antibodies in an animal. After a few weeks, in such cases, the titer drops back again. In still another set of experiments we found that young from a sensitized mother, when nursed by a normal untreated mother, retained a fairly high titer for several months and even showed the rise of titer mentioned. On the other hand, young of an untreated mother when nursed by a sensitized mother acquired a fairly high titer from the milk of the foster mother but lost it rapidly after weaning time. Thus there are evidently constitutional factors operative in the young which have acquired their immunity through the placenta which are absent in the young whose antibodies were conveyed through food.

That changes in the blood serum may be caused by changed conditions in the tissues is further attested by many facts. For example, in pregnancy, the newly forming placenta may set free cells or cell-products which, sometimes at least, cause changes in the blood-serum of the mother, though the exact nature of these changes is

in dispute. Römer, using the complement-fixation technique, found that the serum of adult human beings may possess antibodies for their own lens proteins. Bradley and Sansum, employing anaphylactic reactions, found that guinea-pigs injected with guinea-pig tissue-proteins (liver, heart, muscle, testicle, kidney) develop immunity reactions. Again during the late war, the type of toxic action to which anaphylactic shock conforms was found to exist after extensive injury of the soft tissues. It resulted apparently from the absorption of poisonous substances of tissue origin into the circulation. In fact, various cells and tissues when injured liberate such poisons, and even blood in clotting is known to acquire a transient toxicity of this type.

With facts such as these before us, is it not a rational hypothesis to assume that changes in various parts of a body may on occasion influence the representatives of such parts in the germ-cells borne by that body? This appears all the more probable when we recall the facts learned from the study of precipitins and of anaphylaxis that each species of animal has a thread of fundamental similarity underlying the proteins of all its tissues. There is no reason to suppose that germinal tissue forms an exception. The further fact that homologous tissues, though existing in different species of animals, possess similar chemical characteristics, shows that to get an effect there need not be absolute identity between the protein with which the result is obtained and the original antigen. Since this is so, in order to have a lens antibody affect the germ, there need not be absolute chemical identity between the substance of such a tissue as the lens and the germinal constituents of which it is the expression. And if this is true for lens, why not for other tissues?

The blood-serum of any organism with blood thus affords a means of conveying the effects of changes in a parental organ to the germ-cell which contains the antecedent of such an organ. As long as there is little

change in the somatic element its germinal correlative would presumably remain constant, but any alterations of the soma which give rise to the formation of antibodies or other active agents, particularly if long continued, might induce changes in the germ. Such a hypothesis would seem to be plausible at least in accounting for degenerative changes such as the deterioration of eyes in such forms as the mole, or in fact, in the formation of vestigial organs in general.

On the other hand, there is no reason to infer that changes induced in the blood-serum may not also be instrumental in leading to progressive as well as regressive evolution. If we may have germinally destructive constituents engendered in the blood there is no valid reason for supposing that we may not also have constructive ones. When we learn more about what initiates and promotes growth in a part through exercise, or what causes hypertrophy of an organ, we may likewise find how corresponding germinal antecedents of that part may be enhanced. Until such time we shall probably remain in the dark regarding the mechanism of progressive germinal changes. As already indicated, in the hormones and chalones we have a wonderful series of secretions normally circulating in the blood and maintaining general physiological equilibrium. That reciprocal stimulations of various organs occur by this means is a well-established fact. Hypertrophy or atrophy of an endocrine gland may produce pronounced effects in the furthermost reaches of the body. Again we may inquire, is it reasonable to suppose that the germinal tissues will be inviolate to all this ebb and flow of chemical influence? Should we not expect specific reactions or selections here no less surely than in other tissues? Destruction of the pars buccalis of the hypophysis in the frog-tadpole will cause profound alteration in other endocrine organs such as the adrenals and thyroids, will retard the growth rate, render the entire organism albinous, and produce in the individual pigment cells a condition of sustained con-

traction. Shall we conclude that such a far-reaching influence as this, particularly in a developing organism, will pass the germ-cells by unscathed?

Similarly, growth in man is known to be controlled by a pituitary secretion that is carried by the blood to the various organs. The normal development of secondary sexual characters is determined by products from the testes or ovaries, and the activities of the generative organs themselves are intimately associated with the functioning of the adrenal and other glands. The periods of ovulation are inhibited by secretions from the corpus luteum; lactation is incited by products of the corpus luteum, the involuting uterus and the placenta; the carbohydrate metabolism in the liver and even in the most distant muscles is profoundly influenced by substances formed in the pancreas; the pancreas, liver, and intestinal glands are set to secreting through the stimulus of a product formed in the duodenal and jejunal mucosæ. And still others of such remarkable interrelations can be cited.

Truly one may pronounce that social complex of reciprocating individuals termed cells which make up an organism, "members one of another." And with all of these cooperative activities of the various parts of the body it is inconceivable, to me, at least, that the germ-cells, bathed in the same fluid, nourished with the same food, stand wholly apart.

May we not surmise then that as regards inheritance and evolution, Lamarck was not wholly in error when he stressed the importance of use and disuse of a part, or of modifications due to environmental change, in altering the course of the hereditary stream, particularly if we conceive of these influences as being prolonged, possibly over many generations? Have we not in the serological mechanism of the body of animals an adequate means for the incitement of the germinal changes which underly certain aspects of evolution?

DOMINANCE AND THE VIGOR OF FIRST GENERATION HYBRIDS

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A STIMULATION of growth has come to be recognized as one of the results of hybridization. The phenomenon is of so much importance, practical as well as theoretical, that it has been given a special designation, heterosis. (Shull, 1914.)

New interest has been given to the study of the causes of this increased vigor by the work of Dr. Donald F. Jones[1] (1917 and 1918). Briefly stated the theory accepted by Jones is that growth is affected by a number of different characters or factors, the dominant members of each character pair being favorable and the recessive unfavorable to growth. Each strain or variety possesses some dominant and some recessive characters. When two strains are crossed the first generation of the hybrid exhibits the dominant characters of both parents and is in consequence more vigorous than either parent. In subsequent generations the number of dominant characters in any individual can not be greater than in the first generation and in a large majority of instances will be less, hence the average vigor of the second generation, although still above that of the parents, will be below that of the first.

The theory is not new, but has not been generally accepted because of outstanding objections. Dr. Jones has reviewed the earlier work and has advanced a very ingenious and entirely novel explanation of the objections. This explanation will be discussed later.

Bruce (1910) from purely mathematical considera-

[1] The theory has been further elucidated in the monograph on "Inbreeding and Outbreeding" by East and Jones (1920).

tions, showed that if dominance is correlated with vigor, crossing would produce "a mean vigor greater than the collective mean vigor of the breeds." Only a few days later appeared the paper of Keeble and Pellew (1910) with a concrete illustration and the suggestion that the "greater height and vigor which F_1 generations commonly exhibit may be due to the meeting in the zygote of dominant growth factors of more than one allelomorphic pair." It appears to me unfortunate that in elaborating this theory, Jones has retained the form of statement used by Keeble and Pellew, and describes the phenomenon of heterosis as due to the accumulation of dominant growth factors instead of placing the emphasis on the suppression of deleterious recessive characters. It may seem that the difference is only verbal since a dominant growth factor presupposes a recessive allelomorph. There is, however, a difference in the point of view, especially if the evolutionary significance of the phenomenon is considered. In speaking of dominant growth factors we seem to assume as a starting point, strains of low vigor subsequently improved by the appearance of dominant mutations. It is known that advantageous variations, whether dominant or recessive, are of extremely rare occurrence and while evolutionary progress as a whole must be dependent on such rare progressive changes the effect of these is negligible as a factor explaining heterosis.

Heterosis in Maize

In all varieties of maize there are to be found plants that are abnormal in some particular and these abnormal individuals are almost always deficient in vigor and yield. When varieties are self-pollinated for a series of years at least a large part of the degeneration that follows is caused by these abnormalities.

The bearing of abnormalities on heterosis will be more easily understood if the behavior of two or three examples is described.

A very common abnormality consists of small yellow spots thickly distributed on all the leaves which develop later than the seedling stage. While undoubtedly interfering with the proper functioning of the chlorophyl, the effect of this abnormality is not serious. Even in breeding experiments seed may be saved from a spotted plant and in a population containing these partly chlorotic individuals many of the ovules on the most vigorous plants will be fertilized by pollen from affected plants. It is easy to see how characters of this kind persist.

A more serious and less common abnormality is one that prevents the leaves from unrolling properly, with the result that the plant is bent and contorted and in extreme cases never reaches maturity. Seed would seldom be saved from plants affected with this disorder, but they frequently produce pollen in normal quantities and the character in consequence is widespread and difficult to eliminate.

Albino seedlings may be taken as an example of a still more serious type of abnormality. In this case all individuals that show the character die in the seedling stage. It might appear at first that disorders of this type would be self-eliminating. The character is recessive, however, and in many strains there are plants which are hybrid for the albino character. These hybrid plants show no trace of the character, yet one half of the pollen grains and one half of the ovules carry albinism. If either of these unite with one of their kind an albino plant results, while if they unite with a normal gamete another hybrid plant like the parent is produced. Such characters may be carried along in this manner for any number of generations in a completely latent form, coming into expression only when pollen grains and ovules both bearing the character chance to unite.

Breeding experiments have shown that the more conspicuous of these abnormalities are recessive Mendelian characters which have come into expression through the chance meeting of male and female gametes both bearing

the character. Only a few of the more obvious of these abnormalities have been studied, but there is no line of demarcation between these conspicuous changes and those that are less evident down to variations that can not be distinguished visually from environmentally induced fluctuations.

Different varieties possess different assortments of deleterious characters and in a cross between two unrelated strains all of the recessive lethal or semi-lethal characters[2] not common to both parents are kept from expression, since the recessive characters of each parent are brought into combination with, and suppressed by, their dominant allelomorphs in the other parent. Freed from the depressing effects of these recessive characters, the first generation of a hybrid is usually more vigorous than either parent. In subsequent generations the old recessive characters again come into expression in some of the plants, thus reducing the general vigor below that of the first generation.

If the above explanation of heterosis is to be accepted it should follow that a majority of the departures from the normal must be deleterious and recessive while those which are advantageous are dominant.

The existence, on the other hand, of advantageous recessive, or deleterious dominant, variations would operate to make F_1 populations less vigorous than the average of their parents and conversely inbreeding would tend to increase vigor.

Variations in Maize Chiefly Deleterious and Recessive

None of the recorded Mendelian variations of maize is of a nature that would be advantageous to a wild

[2] The term character has been used in many places in this paper where it would have been more in conformity with current usage to employ the term factor.

Since heterosis results from the combined action of independent units it might seem proper to call these units factors. Taken individually, hovewer, each of the units is assumed to produce a tangible effect and is, properly speaking, a character.

plant and most of them are obviously detrimental. Moreover, if variations occur at random the chances are almost infinitesimal that any particular variation would constitute a favorable addition to the complex mechanism of a highly specialized plant or animal. A chance alteration in the parts of a machine would seldom improve its efficiency.

Of the recorded heritable variations in maize the departure from the normal condition is recessive in a great majority of the cases. Aside from a number of widespread characters where neither member of the allelomorphic pair may be considered more normal than its mate, the only dominant variations in maize that come to mind are pod corn and fasciated or bear's foot ears.

On the other hand, the recessive variations already described number more than 20 and it would be safe to say that hundreds of others are known to maize breeders.

In a complex organism we may expect that deleterious variations will occur more frequently than beneficial variations, but that such a large proportion of the characters should be recessive calls for comment. East and Jones hazard the suggestion that natural selection has suppressed the tendency to produce dominant unfavorable variations while the tendency to produce unfavorable recessive variations has been tolerated.

It should be kept in mind that the observed preponderance of recessive characters does not necessarily imply that a corresponding preponderance of mutations or germinal changes are recessive. Dominant disadvantageous variations are eliminated much more promptly than recessive and the gradual accumulation of recessive characters soon would place them in the majority in any cross-bred species. It seems not improbable that the great preponderance of recessive over dominant characters is a measure of the extent to which dominant characters are eliminated. In a cross-bred form even variations that result in sterility or death may persist indefinitely if recessive. It may well be that the rate at which

dominant characters appear represents roughly one half of the germinal changes that are taking place, new recessive characters originating at approximately the same rate. The preponderance of recessive characters would then be explained, as the result of their preservation in a hybrid condition.

Minor Variations Occur with Greater Frequency than Major Variations

This assumption is made necessary by the fact that the abnormalities which are sufficiently conspicuous to be identified and isolated will account for a part only of the reduction of vigor that follows inbreeding. A part must be due to the combined effect of minor unfavorable variations, the effect of individual variations being insufficient to produce changes that can be distinguished from environmental fluctuations.

That minor variations are more numerous than major is almost self-evident if large and small variations form a continuous series, as they seem to do, since there is a limit to the largeness of variations but none to their smallness. If further proof is needed it follows from the fact that most major variations can be resolved into less comprehensive variations and these subsidiary or minor variations must be more numerous than the major variations of which they form parts.

As East has noted, our classification of variations into large and small may have only a remote relation to the importance of characters in the plant's economy. But whether judged by the change in appearance or by their importance to the organism, it is certain that larger or more fundamental changes must occur less frequently than smaller or less important variations.

The Nature of Variations in Maize

The appearance of deleterious characters when maize is inbred and their disappearance when crosses are made, would follow whether the characters were the result of recombination or of mutation.

There seems to be no sure way of distinguishing between the behavior of characters that appear as the result of recombination and those that result directly from a germinal change. Changes that occur in homozygous strains must be mutations. It is, however, theoretically impossible to be certain that a strain is homozygous regardless of the number of generations that it has been selfed and, practically, the criterion of homozygosity is fixed by the accuracy with which comparisons can be made. With quantitative characters in maize it is difficult to detect with certainty differences of less than 10 per cent., yet sister progenies of strains that have been selfed for as many as 8 or 9 generations usually show differences too large to be ascribed to chance. This difficulty of obtaining uniformity may be due to the large number of factors involved, but also may be due to the frequency of minor mutations. If a new character appears in a relatively uniform strain that has been selfed for a number of generations and the character behaves as a simple Mendelian unit, it usually is ascribed to a mutation. Even in such cases, however, the character may be due to recombination. If the two factors of a dihybrid recessive character arose independently in nearly the same position on homologous chromosomes, the close linkage of the dominant allelomorph of one factor with the recessive allelomorph of the other would long postpone the appearance of an individual with both recessive factors and when it did appear the departure of its behavior from that of a simple character would be difficult to detect.

Although the nature of variations does not affect the bearing which the preponderance of recessive characters has on the explanation of heterosis, there are practical as well as theoretical reasons for wishing to know whether new characters that appear in breeding stocks are mutations or result from the combination of factors already present in the germ plasm. If the undesirable characters that appear from time to time, even in well-

bred varieties, are the result of recombination, the breeder will be encouraged to expend the time and labor necessary to eliminate them. If, on the other hand, these new characters are the result of an unstable germ plasm other means must be sought.

Already the importance of deleterious recessive variations has found application in the breeding of maize. It soon was realized that to successfully eliminate recessive characters it is necessary to bring the characters into expression by inbreeding. Once a strain has been freed of undesirable characters, vigor may be restored by combining the inbred lines or the full advantage of dominance may be realized by growing first-generation hybrids of the better strains.

This method of breeding will be relatively unsuccessful if unfavorable mutations are of frequent occurrence. It is perhaps too early to be sure that this is not the case, but it is encouraging that in strains self-pollinated for 13 generations Jones finds no conspicuous variations after about the 7th generation. The next step is to demonstrate that no unfavorable variations appear when the selfed lines are crossed. This has been shown to be the case in the first-generation, but a certain percentage of multiple factor recessives are to be expected in subsequent generations.

If linkage is operative these recessive characters would come to light slowly, much as they appear in successive generations of an open-bred variety. As already pointed out, there is as yet no way of distinguishing between mutations and multiple factor characters, when the factors are linked.

Nature of Degeneration That Follows Inbreeding.

In discussing the nature and causes of the reduction of vigor that follows inbreeding, it is necessary to choose words with great care. To state the questions at issue in such a way as to distinguish between differences of fact and differences in the use and meaning of words will tax the possibilities of the language.

Many of the older writers on heredity have held that inbreeding is a cause of degeneration. In avoiding ambiguous words "cause" is one of the first that must go. If forced to define their position this school would probably be content with the statement that degeneration is a necessary consequence of inbreeding, the intermediate steps or nature of the process being unknown. Is this conception really at variance with the idea that degeneration results from the increased number of unfavorable recessive characters brought into expression by increasing homozygosity? Does not this conception rather amplify the older, general and indefinite position by explaining how the degeneration may be brought about?

It excites unnecessary opposition, and is not entirely fair, to read into the early writings the idea that inbreeding was held to be the immediate and direct cause of the subsequent degeneration. Such words as "cause" and "per se" have perhaps been used, but is there not sufficient latitude in their meaning to allow the later discoveries to be looked upon as explaining rather than refuting the old doctrine?

In the attempt to bring the two views into sharp contrast the newer explanation is sometimes stated in terms which likewise must be interpreted with latitude if the explanation is to be accepted. Thus East and Jones (p. 123) state one of the results of inbreeding maize as follows: "There is a reduction in size of plant and productiveness which continues only to a certain point and is in no sense an actual degeneration." It is difficult to imagine a degeneration more "actual" than that usually following the inbreeding of maize.

In another place (p. 139) the same authors say: "The only injury proceeding from inbreeding comes from the inheritance received." Such statements have an unfortunate air of finality that probably was not intended. The relation between inbreeding and degeneration has been greatly clarified by the work of these authors, but the above statement taken literally places them in a posi-

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tion similar to that of the older writers who stated that inbreeding was the "cause" of degeneration. There may well be other and important ways in which inbreeding is associated with degeneration.

There is for example definite evidence that vigor is reduced by continued asexual reproduction (Shull, 1912), and although it may be urged that this result is associated with the phenomenon of senescence, so may be the decline of vigor that follows inbreeding.

Furthermore, it has been shown by Calkins (1919) that in the ciliate, *Ursoleptus,* conjugation between sister cells of an asexually propagated line increases vigor.

Objections to the Explanation

Two objections have stood in the way of accepting dominance as an explanation of heterosis. The first of these is that if this explanation is the correct one it should be possible to obtain an occasional F_2 individual, homozygous for all dominant allelomorphs, the progeny of which should be uniformly as vigorous as the F_1. It is held that no such F_2 individual has been found. The second objection is that the distribution in F_2 should be skew with the mode above the mean while in fact F_2 populations show a symmetrical distribution.

Jones has proposed a novel and ingenious explanation of both objections. He has pointed out that it is only necessary to assume that the phenomenon of linkage, which plays such an important rôle in the inheritance of *Drosophila,* is operative also in maize.

If groups of characters are inherited as units with little or no crossing over, both dominant and recessive characters being represented in any particular unit, the first generation would still exhibit all the dominant characters of both parents, but when segregated into pure lines each pure line would again exhibit recessive characters, with a consequent decline in vigor.

This assumption of group inheritance or linkage would also meet the objection that F_2 populations exhibit a normal and not a skew distribution.

There are a number of instances of coherence or linkage known in maize, but if the characters studied to date are a fair sample the rôle of linkage must be of minor importance. Linkage relations have not been studied in sufficient detail even to state with assurance that the characters are arranged in linear series corresponding to the number of chromosomes, although this conclusion is indicated. The linkages of most of the Mendelian characters are very loose and it would seem necessary to conclude that, if the characters of maize are arranged in a linear series, the chromosomes must be either very long or very flexible.

While admitting that linkage would meet the objections urged against the simple hypothesis that the suppression of recessive characters explains heterosis, it may be well first to make sure that any such assumption is necessary. An examination of the maize literature indicates that the difficulty of securing uniform strains with the vigor of the first generation has been assumed rather than demonstrated. No case was found where selection following hybridization had been continued long enough to approximate homozygosity. There are also very few cases where the more vigorous F_2 individuals have been chosen as parents of the F_3. The most extensive series of experiments are those of Emerson and East (1913).

Height is probably the most satisfactory character to use as a measure of heterosis. There are 23 comparisons of F_1 and F_2 populations in the work of Emerson and East. To these six can be added from our own experiments.

In these 29 cases the mean of the F_2 was below that of the F_1 in every instance but in ten of the 29 cases the largest of the F_2 plants equalled or exceeded the largest of the F_1 individuals and in every case where a progeny was grown from a plant near the upper limit of the range of the F_2 its mean exceeded that of the F_1.

Other characters reported by Emerson and East for

which the F_1 was measurably larger than the mid-parental value are length and diameter of ear and length of internode. With respect to length of ear (Tables XIII–XV), there are 13 F_2 progenies that may be compared with the F_1. In 10 the mean was higher than the mean of F_1. Four F_3 progenies were grown from F_2 individuals above the mean of F_1 and in 3 of these the mean exceeded the mean of F_1.

With respect to diameter of ear (Tables XVIII and XIX), 8 F_2 progenies may be compared with the F_1. In 2 of the 8 instances it would appear that the mean was above that of F_1. Seven of the 18 F_3 progenies were grown from F_2 individuals above the mean of F_1 and in every case the F_3 mean exceeded the mean of F_1.

Length of internode is the character showing the most decided increase in F_1 over the mid-parental value. In the two crosses reported (Tables XXXIII and XXXIV) this increase was 33 and 27 per cent. None of the F_2 progenies grown the same season as the F_1 equalled the F_1. The mean of the F_1, however, was exceeded by the mean of 5 of the F_3 progenies grown the following season, although the parents were not selected for internode length. The results with these characters give little or no evidence of non-heritable vigor in the F_1, neither is there any proof that it is difficult to select progenies with the vigor of F_1.

Expectation of Obtaining F_2 Progenies with the Vigor of F_1

In the absence of experimental data, to secure which will require very extensive experiments extending over many years, it may be instructive to consider what results may be expected if suppression of semi-lethal characters is the true explanation of heterosis.

The difficulty of obtaining individuals homozygous for all or even a limited number of characters has been frequently pointed out, but the bearing of this on the difficulty of retaining the vigor of the first generation seems not to have been appreciated.

With a sufficiently large number of characters influencing vigor it would be impossible in practice, even without the assumption of linkage, to obtain homozygous individuals having the vigor of the first generation.

Thus with 10 pairs of characters over 700,000 individuals would have to be grown before there would be an even chance of obtaining an individual homozygous for all of them.

More than ten separately inherited Mendelian character differences affecting growth have been identified and there is no reason for believing that more than a small proportion have been isolated or that more than a small proportion produce conspicuous morphological changes that would be readily detected.

A near approach to the vigor of the F_1 might be expected, of course, without complete homozygosity.

Some idea of the chances of isolating strains that are practically homozygous may be obtained by calculating the size of the populations that must be grown to insure a reasonable chance of finding an individual homozygous for say 70 per cent. of the characters.

Table I indicates the size of the populations necessary to fulfil these conditions with the number of character pairs ranging from 10 to 30.

TABLE I

Number of Pairs of Characters Involved	Number of F^2 Individuals Necessary to Provide an Even Chance of Obtaining at Least One Individual Homozygous for 70–90 Per Cent. of the Character Pairs		
	70 Per Cent.	80 Per Cent.	90 Per Cent.
10	199	1,760	23,400
15	6,000	56,000	16,150,000
20	23,600	1,800,000	429,000,000
25	457,000	39,100,000	28,200,000,000
30	2,470,000	1,710,000,000	7,070,000,000,000

It will be seen that to have a reasonable chance of obtaining an individual homozygous for even 70 per cent. of the character pairs it is necessary to limit the character pairs to 15 or less. Another way of gaining a quantitative idea of the degree of homozygosity that

TABLE II

NUMBER OF F_2 INDIVIDUALS NECESSARY TO PROVIDE AN EVEN CHANCE OF OBTAINING AT LEAST ONE INDIVIDUAL HOMOZYGOUS FOR THE NUMBER OF DOMINANT CHARACTERS INDICATED IN COLUMN ONE.[1]

Number of Dominant Homozygous Characters	Number of Characters Involved													
	2	3	4	5	6	7	8	9	10	11	12	13	14	15
2	11	5	3	2	2	1	1	1	1	1	1	1	1	1
3		45	14	7	4	3	2	2	2	2	2	2	1	1
4			178	45	19	10	6	4	3	3	2	2	2	2
5				710	150	54	26	14	9	6	5	4	3	3
6					2840	516	165	70	35	20	13	9	7	5
7						11400	1820	516	199	94	49	29	19	13
8							44900	6520	1760	584	246	123	68	41
9								182000	23400	5500	1770	700	322	165
10									726000	85400	18400	5490	2030	870
11										2900000	313000	62600	17400	6000
12											11600000	1160000	215000	56000
13												46500000	4320000	750000
14													186000000	16150000
15														744000000

[1] The determinations are carried to only three significant figures.

may be expected is presented in Table II, which gives the number of individuals necessary to provide an even chance of obtaining at least one individual homozygous for different numbers of characters in crosses when from two to 15 character pairs are involved. It should be kept in mind that even though one should obtain an individual homozygous for a sufficiently large percentage of the characters involved to approximate closely the F_1 in vigor, it would be necessary to grow a progeny from this individual before its inherent vigor could be demonstrated. The numbers given in the tables might thus be taken to represent F_3 progeny rows instead of F_2 individuals.

The conclusion is that perjugate progenies equalling or even closely approximating F_1 in vigor are hardly to be expected in breeding experiments and consequently no assumptions are necessary to account for their non-appearance.

SKEW DISTRIBUTION DUE TO DOMINANCE

The second objection, that of the failure of F_2 progenies to show a skew distribution, may now be considered. There can be no question that a series of independent, dominant characters influencing size would bring about a skew distribution. Assuming the characters to have equal effect, two characters would give a distribution of 1, 6, 9, three, a distribution of 1, 9, 27, 27, and with four characters the distribution would be 1, 12, 54, 108, 81. It is apparent that with an increase in the number of characters the skewness becomes less pronounced. It may be of interest to determine whether, with a reasonably large number of characters, the skewness would be detected in populations of the size usually grown in experiments.

With 20 pairs of characters giving 21 classes 1,099,514,627,776 individuals would have to be grown to obtain a representative population. Of this population 99.91 per cent. would fall in the 12 classes with the largest

number of dominant characters. That is, populations of over 700 would have to be grown before there would be an even chance of getting any individuals smaller than those represented in these 12 classes. With ordinary sized populations then the distribution would be fairly represented by the distribution of the 12 largest classes.

The distribution among these 12 classes would be as follows:

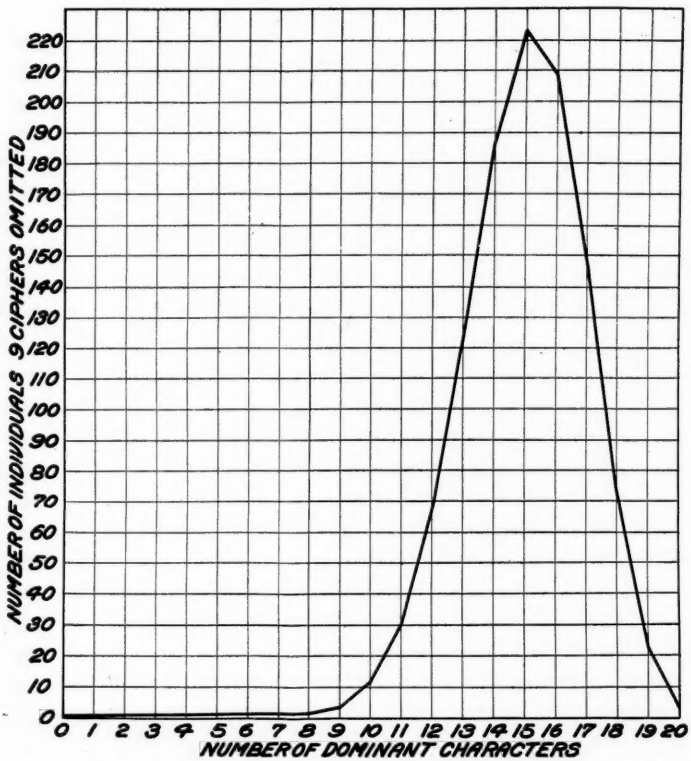
No. Dominant Allelomorphs	Proportion of Individuals Expected
9	.3
10	1.0
11	2.7
12	6.1
13	11.2
14	16.9
15	20.2
16	19.0
17	13.4
18	6.7
19	2.1
20	.3

A distribution of this nature, with populations of approximately 500 individuals, conforms to the normal frequency curve as closely as would be expected. The mode departing from the mean by only 3/100 of a class.

The theoretical distribution of an F_2 population involving 20 pairs of characters of equal weight with complete dominance is shown in the accompanying diagram. It will be noted that although the curve as a whole is skew, the portion to the right of the class with 9 dominant characters, which comprises 99.91 per cent. of the area, is practically symmetrical.

With 10 character pairs there would be 11 classes and 99.65 per cent. would fall in the 7 largest classes and in this portion of the theoretical population the mode would be separated from the mean by only 3/10 of a grade.

Even should it be possible to grow F_2 populations sufficiently large to detect departures from a normal frequency distribution there is yet another reason for questioning that a skew distribution should be expected, when



Distribution of individuals in an F_2 population involving 20 pairs of characters of equal weight and showing complete dominance.

plotted in the customary way. It has come to be accepted that the effect produced by a given growth factor is dependent on the size of the organism. For example, if a growth factor increases the length of the internode by a given amount, it is clear that the height of a plant with 30 internodes will be increased more than that of a plant with only 15 internodes. In other words, the effects are factorial instead of additive. A convenient method of classifying a population on a factorial basis has been proposed by Zeleny (1920), who takes the range of each class as a constant percentage of the value of the mid

point of the class. The result of this change in plotting is to increase the range of sizes included in the higher classes and consequently to raise the mode.

In conclusion it would seem, therefore, that the assumption of linkage, while perhaps not improbable, is superfluous so far as the explanation of heterosis is concerned, since neither of the objections which it was framed to meet have foundation in fact.

It is, perhaps, too much to assert that the suppression of deleterious recessive characters completely explains heterosis or that the reappearance of these characters is the only factor in the decline in vigor that follows inbreeding, but the behavior of maize is in full accord with this explanation.

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CORRELATION OF TAXONOMIC AFFINITIES WITH FOOD HABITS IN HYMENOPTERA, WITH SPECIAL REFERENCE TO PARASITISM[1]

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ENTOMOLOGISTS can all agree that the attachment of most phytophagous species belonging to the more highly specialized orders of insects is very firmly fixed, and the Hymenoptera form no exception. We can also agree, although in less definite terms, that many parallels exist among plant-eating Hymenoptera between taxonomy and food habits. I do not propose to treat of this series, however, partly because I am not sufficiently familiar with them, but also on account of the great interest which attaches to the parasitic groups of Hymenoptera.

During the last decade our conception of the process of nutrition in insects has undergone considerable change, due to the discovery that various microorganisms form an important part of the food supply of many forms. It is quite certain that certain saprophagous, sarcophagous and coprophagous ones probably feed directly, not at all upon decaying and fermenting plant materials, carrion or excrement, but upon the bacteria, yeasts, etc., always abundant in organic material undergoing decomposition. We must judge of the protein requirements of such insects not by the gross substances or substratum, but on the basis of the microorganisms present (Baumberger, '19).

This aspect does not appear to enter into the economy of the Hymenoptera, although there may be a relation between fungi and nutrition in some Cynipidæ, as the

[1] Contribution from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 181.

galls of these insects are commonly invaded by fungi and yeast-like organisms. On the other hand, these same gall-wasps exhibit remarkable correlations between structure and habits as shown by many workers, most elaborately and clearly by the recent studies of Kinsey ('20). The Cynipidæ are at present restricted to a very limited series of plants on which they induce the formation of galls. With the exception of some undoubtedly primitive forms, they occur almost exclusively on Rosaceæ of the genera *Rosa* and *Rubus,* and on the unrelated genus *Quercus,* the latter harboring a very large number and a far greater variety of forms. In the gall wasps, we see, therefore, a nearly exclusive association with a very few genera of plants and what is still more striking is the fact that the more primitive ones, although few in number, exhibit a wide range of food-plants. This leads to the inevitable conclusion that we can trace the evolution of host relations in this group as now living, from a very generalized condition to a highly specialized one.

Many other insects, particularly Homoptera, harbor certain probably symbiotic organisms, and recent studies (Brues and Glaser, '21) tend to show that these may be very important factors in the nutrition of the insects. Almost nothing is known concerning such organisms in Hymenoptera, but if they are present in some cases, as seems probable, they must be reckoned with in any complete studies of food-habits.

The relation of food-habits to taxonomy in the Hymenoptera becomes particularly interesting in connection with the appearance of parasitism in several forms, which is of widespread occurrence in the order. In fact, a large proportion of the Hymenoptera are parasitic, and with the development of this mode of existence have come such elaborate structural modifications, and specialization in behavior, that species have multiplied at a very rapid rate. From this apparent chaos, even taxonomists have as yet brought only very partial order, and any discussion of parasitism in the Hymenoptera is

necessarily very incomplete and may be misleading in some details.

In the Hymenoptera the designation "parasitic" has been applied to habits of extremely diverse nature, and this very loose use of the term may easily lead to serious confusion unless we consider the matter carefully before proceeding further. It is most commonly applied to several large and abundant groups whose members live in the larval condition in other insects which they almost invariably destroy after attaining full growth. Such habits are quite similar to those encountered in other orders of insects, although in no other do they attain such a high degree of specialization; nor do they involve such a series of unrelated smaller groups, with the possible exception of the Diptera. While this is the most abundant and widespread type of parasitism among insects, we must not lose sight of the fact that it is a rather unusual condition so far as animals and plants in general are concerned, in that the parasite and host belong to the same class and are thus closely related. A similar relation exists among the Crustacea where certain decapods are parasitized by other members of the same class, and even among Protozoa there are ciliates parasitic in the bodies of other infusorians. Such associations are very rare, however, and the vast majority of parasitic Crustacea and Protozoa, as well as other parasitic animals, depend upon animals far removed from themselves for hosts, although there is very generally a close correlation between the host and parasite in that related parasites depend upon related hosts. Another peculiarity of this type of insect parasitism lies in the prompt death of the host, which does not usually ensue as a result of other animal parasites, although it is a common result of presence of some protozoan parasites of the higher animals. In others, again, like the well-known nematode, Trichina, the ultimate death of the host is necessary for the continued propagation of the parasite, but actual death normally results from other causes. Still another charac-

teristic of this type of insect parasitism is its restriction to the larval stages, although extending over the entire growth period. This is by no means unique among animals, but it is one of the distinguishing characteristics between this type of parasitism and the one next to be considered. In its perfected state this relation between host and parasite is a marvelously balanced association and one which we might expect to furnish valuable data on the correlation between taxonomy and habits.

A second type of parasitism encountered in the Hymenoptera is that exemplified by most of the parasitic bees and wasps. This has recently been discussed by Wheeler ('19). Here the parasitic larva is really at first predatory so far as food-habits are concerned, devouring the host larva shortly after hatching. The sequence of events is initiated by the preparation of the larval food-supply of the host by the mother bee or wasp. Most solitary wasps store up, in a nest which they have prepared, one or more insects which they have paralyzed by means of the sting, and attach one of their eggs to the body of the prey. Under normal conditions the larva hatching from this egg consumes the prey, attaining full growth, and later completing its metamorphosis. Bees behave in much the same manner, but the store of food in the nest consists of honey and pollen. When parasitism intervenes, the egg of the parasite is also placed upon the food supply, and on hatching, the larva of the host and parasite find themselves in proximity, each ready to appropriate the contents of the nest. In numerous cases that have been studied (Graenicher, '05), the larva of the parasitic form has more powerful jaws than its rival, and encounters little difficulty in destroying it. It now proceeds to consume the food-supply exactly as the host larva would have done, casting off its enlarged mandibles at the first molt. Thus the actions of the larva savor not at all of parasitism, but it is in the fixed habits and instincts of the adult, which require the nests of particular wasps and bees, that the parasitic relation holds.

Correlated with such habits, structural modifications of the body appear, such as the loss of the pollen-collecting apparatus in parasitic bees.

In certain ants there occurs a third type, social parasitism (Wheeler, '04) whereby the young females of some ants that do not establish their own colonies insinuate themselves into the nests of other species of ants, do away with the queen, and take on themselves the function of egg-laying. As the larvæ from these eggs are raised to maturity, they produce worker individuals of the parasitic species which gradually supplant the original population. Finally, the colony becomes pure and maintains itself through its own efforts, giving no evidence of the temporary social parasitism by which it has originated. In a very few cases social parasitism may become permanent with the complete elimination of the worker caste.

The term entomophagous parasite may be applied with some appropriateness to all of the three types described, but is most suitable for the first one, since there the parasite not only consumes its host, but feeds upon nothing else during its developmental stages. By far the largest number of species in the order exhibit this type and it is the only one which I shall consider in any detail.

There are several ways in which such parasitism may have originated, but the question of origin is best deferred until its several phases have been discussed at greater length.

Defining parasitism in its several forms as enumerated on a previous page, we find that there are parasitic genera included in nearly all of the larger groups of Hymenoptera. Thus, the Ichneumonoidæ, Serphoidea and Chalcidoidea, each represented by a number of families, are almost exclusively entomophagous parasites, while in the Aculeata, numerous parasitic genera appear, scattered through a series of families with generally non-parasitic habits. In addition to these there is the primitive family Oryssidæ, now known definitely (Rohwer,

'17) to be parasitic, and a few other families nearly all of somewhat doubtful affinities. Thus of the nearly one hundred families included in the order, between forty and fifty are composed either entirely or almost exclusively of genera with parasitic habits, the remainder being phytophagous or predatory with isolated cases of parasitism, among both the predatory series, and one of the phytophagous ones.

Considering these larger groups, the suborders and superfamilies, more in detail we find that the most primitive of all known Hymenoptera, the suborder Chalastogastra, are phytophagous. Of these, about a dozen families, comprising the sawflies or superfamily Tenthredinoidea, are almost exclusively defoliating forms, feeding in their larval stages on the leaves of various flowering plants. Another family, the Siricidæ, feeds internally on the tissues of woody plants, and, at least so far as food-habits are concerned, there are two other families which form a transition between the sawflies and wood-wasps. It is in the groups above these that the parasitic habit appears, and with the possible exception of one family, the Oryssidæ, to be mentioned later, all these groups are usually associated as a second suborder, Clistogastra, contrasted to the more primitive Chalastogastra. Among them several groups of families, conveniently classed as superfamilies, are three extensive parasitic ones: first, the Ichneumonoidea, comparatively large species comprising about half a dozen families; second, the Chalcidoidea, represented by small or minute species comprising fully a dozen families; third, the Serphoidea another half dozen, mainly very small species. Together with a part of the Cynipoidea, these form the enormous complex commonly known as the Hymenoptera Parasitica. All are quite closely related, but rather easily grouped and distinguished, in spite of certain annectant and aberrant families.

The habits of the several series are also very uniform.

The egg is nearly always laid upon the body of the host or thrust into it, usually the latter, to which purpose the extrusible, stiletto-like ovipositor of the female is adapted with great nicety. Oviposition may take place either in the egg of the host, in the larva, or even in a later stage, and the parasite may complete its development either in the stage of the host in which it is laid, or development may be delayed and not completed till the host has proceeded to a further stage in its ontogeny. Under such conditions the larva is to a great extent passive, although in its earlier minute stages it frequently exhibits (*e.g.*, in certain Serphoidea) great modifications in body form, and develops monstrously specialized jaws or other organs to aid in attacking the massive tissues or yolk-masses of its host.

When such modifications of the young larva are transitory and disappear almost completely after one or two ecdyses, they form a transition to several very clearly defined cases of hypermetamorphosis which have been noticed in certain Chalcidoidea by several observers (Wheeler, '07; Smith, '12, and Brues, '19). In members of two families, the Eucharidæ and Perilampidæ, they have found an active, free-living, first stage larva known as a planidium which is quite similar to the triungulin of the Meloid beetles and the Strepsiptera. Like them, the planidium becomes helpless once it has become parasitic. Great interest attaches to the planidium, but until its distribution is much better known it can not be considered of taxonomic value, especially as quite similar larvæ are known in several other orders of insects. Another series of Hymenoptera, certain parasitic bees, are known through the researches of Graenicher ('05) and others to possess much larger jaws in the first larval stage. As we have mentioned previously, the type of parasitism in this case is very different, for the parasite simply eats the host larva that it may appropriate its food-supply, and we have a parallelism in structure, of

independent origin, and hence of no classificatory importance.

Comparative anatomy and post-embryonic development show very clearly that, with the exception of some secondarily phytophagous forms, only the primitive Hymenoptera are phytophagous. As one can not seriously question the monophyletic origin of the order, the varied food-habits now represented must have been derived from some form of vegetarianism.

In all of the higher Hymenoptera or Clistogastra, active and aggressive characteristics are very prominent in the behavior of the adult females, whatever may be the food-habits of the larvæ. Thus in the wasps, the parent captures as prey suitable insects with which to feed her larvæ, or to provision her nest, if her young are to receive no post-natal care. In all cases she prepares some sort of a cell or nest for her brood, and frequently this requires marvelous skill in the selection of particular materials and the collection of specific insects for food. Where nests are provisioned in advance, the prey is stung and paralyzed after a manner that requires very complex instinctive behavior. If, on the other hand, we look at the activities of the larva of one of the wasps that stores a paralyzed insect away and places her egg upon it, we see the larva consuming its food supply much after the fashion of an externally feeding entomophagous parasite. In fact, it is difficult to distinguish any really fundamental differences. In each case the host is stung and the egg attached to it, always externally by the wasp, but sometimes externally also by the parasite. The wasp paralyzes her prey, which the parasite does not do, as her sting is not so severe, and she does not further bother with the host insect. The egg of the parasite is deposited at the time of stinging, and that of the wasp by a later operation of the same organ, the ovipositor with which she has previously paralyzed, but not killed, her prey. Thus, aside from the maternal instincts, the entomophilous wasp is scarcely more different from the ichneumon-

fly, than some ichneumons from others.[2] Equally varied habits exist in at least a few cases even in a single species of ichneumon, for certain Itoplectis may be either parasites of caterpillars, hyperparasites, or inhabitants of the egg-cocoons of spiders where they devour the contained eggs. From the entomophilous wasp has been developed the parasitic one and we have alluded to its origin as traced by Wheeler ('19).

From the foregoing, it is seen that we might derive the habits of the wasp from those of the parasite, or *vice versa*, with but little difficulty, although the more elaborate instincts of the wasp appear more naturally as the latter development.

If now we return to the free-living phytophagous Chalastogastra, it appears for morphological reasons especially that the entomophagous ichneumon flies have been derived directly from them and I think that the transition from phytophagy to parasitism is quite clear. Whether it involves the interpolation of predatism or sarcophagy is perhaps more a matter of conjecture.

The Siricoidea of the Chalastogastra, on account of their legless, eruciform, lignivorous larvæ and reduced wing venation appear to have been derived from some sort of ancestor with a caterpillar-like larva having the more complex wing-venation seen in the saw-flies or Tenthredinoidea. So far as is known, no member of either group is parasitic. Until recently the family Oryssidæ has been regarded as a degenerate group quite closely allied to the Siricidæ. Rohwer has, however, shown that they are really very different and finally (Rohwer, '17) regarded them as a distinct suborder of Hymenoptera. It seems reasonable to suppose that they have Siricid-like ancestors, and as they are now known definitely to be parasitic on the larvæ of wood-boring Coleoptera, it ap-

[2] This matter, as well as several others discussed in the present paper, have been recently dealt with by Picard in a publication (La faune entomologique du figuier, '19) which I unfortunately did not see until too late to refer to it in the text of this article. Picard's "Considérations sur les parasites," pp. 166–172, are of extreme interest.

pears that we have in them the most primitive parasites in the order Hymenoptera. The hosts of the Oryssidæ consist partly, although probably not entirely, of Buprestidæ, which paleontology shows to be an ancient family. Handlirsch ('08) has even gone so far as to suggest that the parasitic Hymenoptera may have been derived from the Jurassic Pseudosiricidæ which no longer laid their eggs in wood, but in the eggs of beetles occurring in the wood. This is entirely speculative and so I think must be at the present time any suggestions as to how the Oryssidæ, or the Ichneumonidæ, which Handlirsch had in mind, became parasitic. That their larvæ first found and fed upon their hosts after hatching seems much more probable. It must be said, however, that predatory or carnivorous Chalastogastra are not known among living forms, except certain adult sawflies which fed in this way (cf. Mrázek, '09). From this point onward we have little trouble in tracing the probable origin and relationships of the Ichneumonoid families as I have attempted to do in a previous paper (Brues, '10). Thus the Stephanidæ are structurally primitive and strikingly like the Oryssidæ in the peculiarly horned head which had been remarked on before the habits of the Oryssids were known. On account of the presence of a costal cell in the wing, the polymorphic family Evaniidæ is necessarily also more primitive than the Ichneumonidæ or Braconidæ, and, through one subfamily, the Fœninæ, resemble the Stephanidæ as has been already noted by Bradley ('08). Some Braconidæ, the Stephaniscinæ, Spathiinæ and Hormiinæ are much like Stephanids, so much so that it is difficult to believe that they are not directly derived from them. One other family, the Capitoniidæ, recently segregated from the Braconidæ, appears to be very definitely related to the more generalized Evaniidæ (Aulacinæ). Omitting in this brief consideration several less pertinent families, and ignoring other recently segregated ones, we have left only the Ichneumonidæ, related possibly through the Alysiidæ to

the Braconidæ. Structurally this relation seems plausible, but as the Alysiids attack almost exclusively the highly specialized Diptera it is very difficult to regard them as closely related to the ancestors of the Ichneumonidæ, so highly diversified in habits and structure. The latter then are not so easily derived and may go back to Evaniid-like forms.

One extremely interesting fact in connection with the primitive families of parasitic Hymenoptera is their association with wood-boring insects. Thus the Oryssidæ, the most generalized group of Evaniidæ, the more primitive Braconidæ, many of the structurally primitive Ichneumonidæ, and the Capitoniidæ are restricted to hosts having such habits. This shows undoubtedly that such habits have not easily been changed and that similarity of host-habits is an important factor in determining what insects may be attacked. This supports strongly our thesis of the interrelation of taxonomy and habits.

In connection with the parasitism of certain chalcisflies, the French entomologist Marchal ('98) discovered, some years ago, a most anomalous method of precocious multiplication which he designated as polyembryony or germinogony. In species exhibiting this phenomenon, the embryo becomes dissociated into a large number of parts, and from the numerous germs thus produced there is formed a veritable swarm of minute parasites, the extent of which is limited only by the available food supply in the host. Marchal's first observations have been much extended since by himself and numerous other workers, and the same condition has been found to exist in many other Chalcidoidea and also in the Serphoidea (Marchal, '03). It has recently been recognized in another widely different family, the Dryinidæ by Kornhauser ('19) and probably occurs sporadically in several other parasitic families, although I believe no other cases have been absolutely substantiated. From the regular association of numerous individuals in single hosts in the case of *Microgaster,* allied genera of the Braconidæ,

and in *Sphæropyx* (Cushman, '13), in a few Ichneumonidæ (*e.g.*, species of *Cryptus*) and in a few Bethylidæ, it would seem likely that they also are polyembryonic.

The widespread occurrence of germinogony and its apparently erratic distribution show that it can be of no general taxonomic interest at least as an aid to classification. It is indeed quite the opposite, for the development of the egg in the process of fragmentation is so similar in the Chalcidoid and Serphoid that we might be led to believe it of common origin. As their ancestors were undoubtedly not polyembryonic, such can not be the case and the process must have originated independently, just as it has in several totally unrelated animals like certain annelids (*e.g.*, *Helodrilus*) which exhibit it in an imperfect condition (Weber, '17) and in the armadillo (Newman and Patterson, '10) among mammals where it has become completely established. A quite similar modification of development is seen in the formation of the rediæ in the sporocysts of Distomes. Still similar, but delayed until the larval stage, is the process of pædogenetic multiplication in the Cecidomiid fly Miastor (*cf.* Felt, '11), well known to all entomologists.

It appears from any general survey of the habits of the parasitic Hymenoptera that we find certain taxonomic groups of host commonly attacked by discrete groups of closely related parasites. It is natural that such combinations should impel our attention, as they may be fitted with the least effort into a classified scheme, and furthermore their mere recurrence is sufficient to indicate that they are not due merely to chance.

The following list includes a few striking instances of this sort drawn at random from widely separate sections of the order:

Parasites	Hosts to Which They are Restricted
Families	
Alysiidæ	Dipterous larvæ.
Trigonalidæ	Vespidæ.

Subfamilies	
Evaniinæ	Cockroaches and their oöthecæ.
Ichneutinæ	Saw-fly larvæ.
Genera	
Polygnotus	Cecidomiid larvæ.
Coccophagus	Soft scales.

If we should reverse the order of the above list and attempt to tabulate groups of related hosts that are affected only by certain groups of parasites we should have great difficulty in finding examples. This, of course, is to be expected on account of the passive condition of the host and the active rôle of the parasite, whereby it first came to infest some certain kind of host. Inheritance of such specific instincts over long periods of time, during which groups were becoming differentiated, will lead naturally to the evolution of groups of parasites attached to groups of hosts which have meanwhile been developed. Such reasoning appears to be sound and may explain some of the conditions tabulated above.

I think, however, that there is a deeper basis than this, and that we can not fully understand such combinations without inquiring into the actual physiological relations between host and parasite.

It has been customary among entomologists to place great emphasis upon the maternal instinct of invariable selection as determining and restricting the range of hosts affected by specific parasites. Among zoologists who deal with other parasites, particularly Protozoa and lower invertebrates, no such idea has ever been entertained, as the parasite plays a passive rôle in attaining its host. The malarial parasite is ingested by all insects that suck human blood, but is able to continue its parasitic life only in certain particular mosquitoes. Similarly, a certain Cestode worm parasitic in birds has as intermediate host, the garden slug, from which the definitive host obtains it by eating the slug. That this Cestode does not occur in other hosts that may eat infected slugs is a phys-

iological matter and is always regarded as such by helminthologists who encounter many instances of this kind. On account of the definite requirements of such parasites, Cobb ('04) suggested some years ago that they might give valuable clues to the taxonomic affinities and physiological peculiarities of their hosts, the latter particularly in cases where there is a wide range of hosts.

In insects, and, quite fortunately for the present discussion, in the parasitic Hymenoptera, there are available some extremely pertinent observations made by Timberlake ('12) relating to the fate of eggs in the bodies of host insects in which they do not normally develop. His experiments were made with an Ichneumonid, *Linnerium validum,* commonly parasitic in caterpillars of the fall web-worm. This parasite will also oviposit in larvæ of various other moths, when persuaded to do so in captivity, by depriving it of its normal host; but it can not complete its development in the experimental hosts. This is due to the death of the young larvæ, which succumb to the reactions of the host soon after hatching, or possibly in some cases even before hatching. The antagonistic action of the tissues of the host is manifest by the accumulation of amœbocytes about the unwelcome objects. In one other abnormal host, the tent-caterpillar, this *Linnerium* may survive and complete its transformations, but there is a high mortality among the parasites, for many are destroyed by the host.

These experiments show very clearly why this parasite is restricted to certain hosts and, from the nature of the reaction, which is so similar to that exhibited by animals in general toward microorganisms and other foreign materials, there is little reason to doubt that insects usually react in this fashion. This also furnishes an explanation for the continued restriction of parasites to specific hosts, based upon natural selection, since individuals choosing unsuitable hosts will suffer a very material reduction in the number of their immediate progeny. This is, I think, especially important, as it takes much of the burden from

the already greatly strained principle of the fixity of instinct in the imaginal insect.

It also aids greatly in understanding the relation previously referred to, where extensive groups of parasites attack discrete groups of host. Adaptation to one host means ordinarily greater physiological suitability for another closely related host than for a widely different one. This, no doubt, applies to cases like the Alysiid parasites, for here the series of hosts, while quite uniform, is so extensive that it can not be explained on the slowly acting basis of concomitant differentiation of the hosts and parasites.

Instances, like one cited by Pierce ('08) where several species of parasites suddenly became abundant enemies of the boll-weevil due to the scarcity of their more favored hosts, must depend upon selection, as suggested above, leading to the rapid improvement of partial adaptations.

We have already referred to the fact that the parasitic Hymenoptera, and quite generally also most parasitic insects, attack other insects, and pointed to this as a characteristic more or less peculiar to insect parasitism or at least to its most prevalent types.

The attachment to closely related animals as hosts is shown still more clearly in Hymenoptera that are secondary parasites on parasitic species of the same order, of the same family, or even of related genera. This phenomenon is not restricted to Hymenoptera, but is most extensively exhibited by them. Thus certain genera of Ichneumonidæ, Braconidæ, and Chalcidoidea develop regularly in the larvæ of primary parasites which become established in a free living host.

Secondary parasites are not absolutely distinct from primary ones in some individual cases, for this relation is known to be facultative in a few species of Hymenoptera which develop in either way. In 1903, Fiske ('03) showed from careful breeding experiments that certain Ichneumonidæ of the genus Itoplectis may be either pri-

mary or secondary parasites of the tent-caterpillar, attacking a member of their own family in the latter case. Since then other examples have come to light, but they are by no means common. Another fact which is significant in connection with secondary parasites is that they are very generally much less particular than primary ones in restricting themselves to a small series of hosts.

In searching for the origin of secondary parasitism, it is certain that it must be derived from the primary form, since it is naturally dependent upon the latter for its mere existence. The only other possibility appears to be the assumption that the primary parasites were free-living forms when first parasitized, and that they have since developed parasitic habits of their own. As the secondaries are frequently structurally reduced such a supposition appears still more improbable.

If, then, secondary parasites are derived from primary ones, what can have caused them to desert their free-living hosts? We have already seen how the restriction of hosts among primary parasites seems to have a physiological basis, in that the reaction of the tissues of the host has been shown (Timberlake, '12) to eliminate parasites not adapted to it. In attacking insects very closely related to themselves parasites should stand a much better chance for successful growth, as the physiological antagonism of all animals toward closely related forms is much less than that toward very different ones. Young larvæ of parasitic species should therefore meet with less difficulty in developing in the bodies of related forms, and secondary parasitism might arise with little difficulty when eggs were placed in another parasite rather than in the body cavity of the free-living host. This explanation may account for the prevalent type of hyperparasitism, but not for cases like that of the Chalcidid *Dibrachys* which attacks Hymenoptera and Diptera alike. This may simply be a case of great adaptability in certain species like some mentioned in connection with pri-

mary parasitism, although it may depend upon a general similarity in the tissues of all entomophagous parasites, or a less aggressive condition of the tissue in parasites due to their generally secluded and protected environment. As the latter condition seems not unlikely, it probably acts regularly to make hyperparasitism an easily acquired characteristic.

Striking divergencies, like the following, noted by Swezey ('08), are of interest in this connection. In his studies of Dryinid leaf-hopper parasites, he found a Ceraphronid parasitic on a species of the related Dryinidæ, although the group normally and abundantly parasitizes entirely different types of insects.

The adaptation of animals and plants in conformity with the demands of diverse environmental conditions is now an axiom among biologists. From its manifestations it is evidently a physiological adjustment which leads secondarily to structural changes, and many convergences in form and function are traceable to it. On account of the close interdependence of plants and insects it appears, in some instances at least, to exert an indirect influence upon phytophagous insects (Brues, '20), whereby a species may feed rather indiscriminately on herbs, and another on woody plants, but not upon the two in combination.

In the case of parasitic Hymenoptera there are many instances which might be cited where environment appears to have exerted a direct influence upon the acquisition of host relations and others where we must, I think, believe the influence to be indirectly related to the environment through a second insect, the host. This rather obscure statement may be clarified by a few examples. From what we have said in connection with hyperparasitism, it seems quite clear that a species which may assume the rôle of either a primary or secondary parasite, responds quite directly to the environment, in this case the primary host, which may be either sound or already infested by a parasite which is in turn at-

tacked. This influence seems to be a rather direct one. On the other hand, I may quote from a previous paper (Brues, '08) the following: "The European Chalcid-fly, *Ormyrus tubulosus,* has been minutely studied by Mayr, who has bred it from no less than 27 species of Cynipid galls, and I have from Massachusetts what is apparently the same species, bred from about half as many North American species by the late Dr. M. T. Thompson. The galls formed by the various hosts of this species are many of them entirely dissimilar in form, the only resemblance between them, aside from their gross gall-like form, being their more or less uniform habitat attached to twigs and leaves." Howard ('91) mentions *Enrytoma rosæ* as having over 50 cynipid hosts. A range of hosts of this sort appears to be due not directly to the environment of the host, but to the similar physiological condition of the various Cynpids themselves, which, as we have already said, are closely confined to a very narrow range of food-plants.

The great difficulties occasionally imposed upon parasites in attaining their hosts may be purely a matter of environment, as illustrated by the following considerations.

An interesting series of parasitic Hymenoptera are those which prey upon aquatic insects. In several well-known cases, the behavior of the adult parasites has become so profoundly modified that the females not only enter the water in search of their hosts, but they may be, occasionally at least, accompanied by the males. The first observation of this sort was made nearly a century ago by Francis Walker ('36) on *Agriotypus,* and the well-known observer Sir John Lubbock ('63) later gave an account of the habits of two aquatic Chalcis-flies in which he describes the actual process of swimming. One species, the Mymarid (*Cataphractus cinctus*) makes use of its ciliated, paddle-shaped wings for this purpose, while the other, a Trichogrammid (*Prestwichia aquatica*) propels itself by means of the legs. Numerous other contribu-

tions, notably those of Von Siebold ('58), W. Müller ('89), Marchal ('00), Rousseau ('08), Heymons ('08), Schulz ('07, '10[a], '10[b]), and Matheson and Crosby ('12), have added much of interest, not only in bringing to light aquatic members of several families, but in determining some of the host species upon which they prey. In many cases the adaptation to aquatic life is not so perfect as the cases just mentioned, although several other species are known to swim readily, using either the legs or wings, which usually show modifications adapted to such behavior.

In view of the frequent occurrence of aquatic imaginal forms in other orders of insects such as the Coleoptera and Hemiptera, it is perhaps not surprising to find certain parasitic Hymenoptera adopting this habitat. Viewed more in detail, however, the matter is quite a different phenomenon. Such Coleoptera as Gyrinidæ, Hydrophilidæ, Dytiscidæ, etc., are uniformly aquatic in both preparatory and imaginal stages, and such is also true of the brachycerous Hemiptera. All of these insects are highly modified to conform with their aquatic environment, particularly in reference to the functions of locomotion and respiration.

In the aquatic Hymenoptera, a series of families is represented and only a comparatively small number of genera are included. The structural modifications are far less profound, indeed they frequently represent very slight changes. They are more closely parallel to the natatorial habit shown in isolated genera such as the rice water-weevil, *Lissorhoptus simplex*, a beetle that has become aquatic and oviposits in the roots of the rice plant (Tucker, '12). It has been shown experimentally by Szymanski ('18) that many terrestrial insects may be induced to swim if submerged and we may easily suppose that the truly aquatic habit of the parasitic Hymenoptera just mentioned may have arisen through the seeking of their hosts in aquatic plants, first at or above the surface of the water, and later through a search for further indi-

viduals below the surface. Even memory could easily play a part here, if the host were submerged during the development of the parasite, and the latter emerged as an adult below the water, from which it must escape by locomotion through the water.

In the case of aquatic Hymenoptera, it is readily seen that we can not correlate taxonomy with habits according to any generalized scheme, although the several genera show structural characters associated with their unusual habits. Most striking is the number of Mymaridæ and Trichogrammatidæ included, minute insects whose wings are naturally well suited for swimming.

Frequently a secluded habitat acts as a powerful factor in restricting the kinds of parasites that can attack certain types of hosts. Thus, wood-boring insects can be reached only by species provided with long ovipositors. Such restrictions are clearly defined and many other examples might be cited. Partial inaccessibility of the host may even occur in the case of parasites otherwise well suited to their host, as for example in the case of a common parasite of the eggs of the gipsy moth, which is able to oviposit only in the eggs occupying a superficial position in the egg-mass of the host. Sometimes difficulties may be overcome by the presence of an active first-stage larva. This may exhibit most extraordinary behavior as has been described by Smith ('17) in the Chalsis-fly, *Perilampus*. Here the *Perilampus* egg is deposited and hatches away from the body of the host as a planidium which later attaches itself to the host and remains there till the host completes its growth, after which the planidium begins its parasitic life. A second species that is a hyperparasite seeks out the primary parasite in the caterpillar host through which it bores its way and there awaits the exit of the primary parasite before proceeding with its development.

Again, the female of some egg-parasites attach themselves to individuals of the host species and are thus carried to the place where the eggs within which they will

develop are to be deposited. Certain Chalsis-flies and Serphoids have adopted this curious method of transportation (Brues, '17) which occurs sporadically in diverse insects (Banks, '11). The way in which many modifications of this kind appear in similar form makes it impossible to consider them as guides to taxonomic affinity. The elongated ovipositor, the active first-stage larva, and many other adaptations for attaining the host are of course good taxonomic characters, but they reappear independently in more than one group, and can be used only in combination with characters of less vital importance to the animal, to characterize completely any extensive groups. Nevertheless, the lengthened ovipositor can be used to separate numerous families and smaller groups in the parasitic Hymenoptera and as it bears a certain relation to habits, the latter are thus reflected in taxonomy on a structural basis. However, the habits of many such insects do not seem to require such a long ovipositor and represent not the primitive habit for the group, but recent modifications which break down the homogeneous correlation of structure and habits.

Closely connected with the specific association of natural groups of hosts and parasites is the great variation shown by different parasites in the number and diversity of the species that serve as their hosts. Just as we can find among phytophagous insects, omnivorous forms, strictly monophagous ones, and all intergrades between the two, so there exists among parasites an almost equally varied series of associations with one, several or many hosts.

Although parasitic Hymenoptera are so abundant, both in species and individuals, their food habits are not so easily observed as those of plant-eating insects and our knowledge concerning them is far less complete. The large number of secondary parasites also lead to confusion, as these may not always be distinguished on a structural basis.

If parasitism demands a nice physiological adjust-

ment, we might expect to find that egg-parasites affecting the organism at an earlier and less highly differentiated stage of ontogeny, are more catholic in their tastes. This is, however, not borne out by observation to any extent, and egg parasites are usually as closely restricted to particular hosts as their relatives who confine their attention to larval insects.

Small size is a prerequisite of all true, internal egg-parasites except a few that occur in the oothecæ of cockroaches, where the comparatively large species of *Evania* undergo their development. Some parasites oviposit in the host-egg, but live at the expense of the larva; they are, except in polyembryonic forms, larger, and not classed as egg-parasites.

On the basis of size, then, practically all egg parasites are either Chalcidoidea or Serphoidea and this habit characterizes a number of families, and smaller taxonomic groups (*cf.* Girault, '07, '11). Among them the strange, tropicopolitan genus *Podagrion* attacks only the eggs of Mantidæ. The large cosmopolitan genus *Telenomus* occurs in the eggs of various insects, mainly Lepidoptera while the very similar genera *Phanurus* and *Trissolcus* are restricted to eggs of Tabanidæ and Pentatomidæ. Again, *Scelio* and several related genera attack only the eggs of the Orthoptera Saltatoria. Thus, if used with due caution, egg-parasites are in the main illustrative of close correlation between the taxonomy of host and parasite in spite of the fact that we may naturally regard insect eggs as more similar *inter se,* than insect larvæ.

It is true that the ubiquitous little *Trichogramma* affects eggs of several orders and many families of insects, but like other less conspicuous examples, it stands quite apart from its commonplace associates.

With their larger and more variable size, and great diversity in habits and structure, larval insects present a correspondingly varied series of opportunities for parasites. We find also that practically no genera are known

to parasitize both eggs and larvæ, although the polymorphic and widespread *Eupelmus* among the Chalcisflies appears to be an exception. As the eggs and larvæ of many insects frequently occur together at the same time, this fact is rather surprising and shows that the parasitic association must depend greatly upon gross form, as well as upon the factors of environment and specific physiological reactions, which we have already mentioned. One case which comes to my mind in this connection is quite instructive and there are no doubt others of a similar nature. All the several genera included in the Evaniinæ are, as previously mentioned, parasites in the egg-cases of cockroaches, with the exception of a single reliable record (Picard, '13) of the rearing of *Zeuxevania* from the body of the blattid itself. Quite likely the future may bring forth other similar observations on Evaniines, but this one shows that parasitism has been transferred to the cockroach from the oötheca, which is of course carried about by the female for some time before deposition.

Larval parasites have been more extensively reared than those living in eggs and their habits are consequently better known. Many observations upon individual species of hosts show that the larval stages harbor a far more extensive series of parasites (*e.g.*, Howard and Fiske, '12) than the eggs or pupæ, while hymenopterous parasites of the adult are almost unknown. Among larval parasites it is easy to recognize two general series, so far as the number of hosts utilized. Some species are very conservative in this respect and others extremely versatile. These two terms are equally suitable for genera and larger groups, and the difference is more important when it involves all or most of the species of quite extensive groups. Thus the highly modified members of the family Dryinidæ (Perkins, '05) are restricted to several families of Homoptera. A few which parasitize Membracids are insects of quite ordinary appearance, but the remainder affecting Tettigoniellids and

Fulgorids have the fore tarsi of the females misshapen to form chelæ or pincers, by means of which they cling to their host. Such structures are elsewhere unknown among insects. The group has become highly specialized, apterous in several genera, and has probably reached the end-stage in its evolution. Like all creatures which have attained this condition, it shows no further adaptiveness in habits. This is a clear-cut case of correlation between habits and taxonomic affinities.

Versatile groups naturally include large numbers of genera and species with varied habits which enable them to grasp every opportunity to earn (or, in the case of parasites, to steal) a livelihood. Numerous species and varied habits, are as inseparable as form and function. The former binary involves an added series of factors, since any group of insect parasites comes into keen competition with the members of other groups as it reaches out for new hosts. Some have spread widely among hosts of very similar types, restrained by some insuperable obstacle, probably physiological in nature, from attaching themselves to strange insects. They show a correlation between habits and structure. Others have broken their fetters more quickly and completely, and adaptations in habit have far outstripped structural modifications, resulting in natural taxonomic groups which show only imperfectly such correlation.

The climax in this direction is reached by certain groups which have cast aside parasitism entirely and become phytophagous. This has occurred independently in several families of Chalcis-flies, a group in which the struggle for existence must be very severe. One of these aberrant series, *Megastigmus* and its allies (Crosby, '13) feed within the seeds of plants, mainly those of various trees, upon a rich protein diet, probably similar to that of their entomophagous forebears. Another, *Isosoma* and its allies (Howard, '91 and '96; Phillips and Emery, '19) occur in far less delectable vegetable tissue, such as the culms of grasses in which they sometimes cause

galls. A third (Mayr, '05), including some genera related to the remarkable parasitic *Perilampus,* which we mentioned a few moments ago, produce conspicuous galls on certain plants.

The production of galls by the phytophagous Chalcids is quite suggestive, since many forms related to Isosoma (*Harmolita*) are parasites of gall-making Cynipids. *Megastigmus* also belongs to a group including many parasites of Cynipids. Since we do not know exactly how galls are formed, however, the matter can not be profitably discussed at the present time.

Although they may not aid us greatly in formulating any general causes leading to divergence in habits among related forms, I should like to append a few observations made by various entomologists which suggest a variety of factors.

The effect upon the parasite of almost complete elimination of a host through excessive parasitism has often been commented upon by entomologists. An especially clear case has been described by Aldrich ('12) where an invasion of the western pine-butterfly was suddenly checked by *Theronia fulvescens.* The parasite then found it necessary to eke out an existence from scattering and less suitable forest insects and under such stress, selection must be very keen (cf. p. 147). Complete parasitism of 100 per cent. of the related cabbage butterfly by *Apanteles glomeratus* has also been reported by Chittenden ('05).

Errors or aberrations of instinct have also been occasionally observed. Thus Marchal ('07) saw a Chalcidid parasite of coccinellids (*Lygellus*) repeatedly oviposit in the pupal exuvia when living material was not available. Still more incongruous is the behavior of *Trichogramma* observed by Holloway ('12) who found this insect actually ovipositing in small globules of partly solidified plant juice on the foliage of okra plants. One of the common hosts of this egg-parasite, the cotton boll-worm, frequently oviposits on the leaves of okra and the globules

were evidently mistaken for moth-eggs. Premature oviposition is generally attributed to physical necessity in relieving the pressure in the body, but here at least it is accompanied by the outward appearance of instinct. Whether this Chalcid tasted the strange new host is not stated, but it is a common procedure among Chalcids (Howard, '10) to tap the host with the ovipositor, and to lap up the exuding body-juices quite independently of egg-deposition. What her reasons for this may be are obscure; possibly it is to test the suitability of the host; perhaps to secure food, or she may even retain a specific appetite for the kind of food consumed in her earlier days.

Marchal, Vayssière ('07) and Loiselle ('08) have commented upon the retarded development observed in certain Ichneumon-flies whereby emergence of some individuals was delayed a year. Such occurrences might serve to bridge over the gap of a season when host insects were scarce; on the other hand, if the time were not exactly twelve months it easily might lead to a new "trial" association in the absence of the proper host at that season.

That these factors might lead to divergence in habits, I can not doubt, but hesitate to apply them to any concrete cases of aberrant habits.

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ONCE MORE THE SUCKING-FISH

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IN 1919, while Professor E. W. Gudger's excellent series of articles "On the Use of the Sucking-fish for Catching Fish and Turtles" appeared in THE AMERICAN NATURALIST, I was at work on my first volume of "Africa and the Discovery of America," where I had to touch on the remora story in the early voyages to America, in order to show that they were all a myth, based on the literary influence of Odoric of Pordenone on Columbus. As my sources were naturally of a different character from those of Professor Gudger, who was chiefly interested in the zoological side of the question, I was able to supplement his thorough discussion with a number of new data, which the zoologist will not consider to be amiss.

The remora was dimly known to all the Arabic voyagers. We meet with it in the middle of the ninth century, in the very beginning of the "Chain of Chronicles."[1]

In the Indian Ocean there is a fish, twenty cubits in length, in whose belly there is a fish of the same kind, in whose belly there is similarly a third fish. All these fishes are alive and moving. This large fish is called *al-wāl*. In spite of its size it has for its enemy a fish only a cubit in length, called *el-leshek*. When the large fish becomes angry and attacks the other fishes in the sea and maltreats them, the little fish takes charge of him: it attaches itself to the root of his ear and does not let go of him until he is dead. The little fish also attaches itself to boats, and the large fish dares not approach it, because of the fear with which it inspires him.

[1] M. Reinaud, "Relation des Voyages faits par les Arabes et les Persans dans l'Inde et à la Chine dans le IX^{e} siècle de l'ère chrétienne," Paris, 1845, Vol. I, p. 2 f.

This account is obviously an exaggeration of some story about the shark, but *wāl* was soon identified with the whale, as appears from the later Arabic sources. A century later Mas'ūdī wrote:

There is a fish in this sea called el-Owāl, which is from four to five hundred 'Omari cubits long; these are the cubits in use in this sea. The usual length of this fish is one hundred perches. Generally the head of the whale is out of the water; and when it powerfully ejects water, it gushes into the air more than one bowshot high. The vessels are afraid of it by day and night, and they beat drums and wooden poles to drive it away. This fish drives with its tail and fins other fish into its open mouth, and they pass down its throat with the stream of water. When the whale sins God sends a fish about one cubit long called *esh-shak* (*al-leshek, as-sal*), it adheres to the root of its tail and the whale has no means to make itself free from it. It goes therefore to the bottom of the sea and beats itself to death; its dead body floats on the water and looks like a great mountain. The fish called *esh-shak,* adheres frequently to the whale. The whales notwithstanding their size, do not approach vessels; and they take flight when they see this little fish, for it is their destruction.[2]

Idrīsī merely said that in the Sea of Oman the *wālī,* which is of white color and one hundred cubits in length, is usually accompanied by the small *leshek,* which kills it.[3] Ad-Damīrī definitely identifies the large fish with the *bāl,* the whale.

When it begins to tyrannize the other animals of the sea, God sends a fish about a cubit in length, which attaches itself to its ear, and the *bāl* seeing no means of freeing itself from it, goes down to the bottom of the sea and strikes its head on the ground until it dies, after which it floats on the top of the water like a big mountain, and the men on the East Coast of Africa are generally on the look-out for it. When they find it, they plunge harpoons on it and drag it to the shore where they cut open its belly and take out of it ambergris.[4]

The important point in all these stories, which obviously emanate from the same original account, is that

[2] A. Sprenger, "El Mas'ūdī's Historical Encyclopedia, entitled 'Meadows of Gold and Mines of Gems,'" London, 1841, Vol. I, p. 263 f.

[3] P. A. Jaubert, "Géographie d'Edrisi," Paris, 1836, Vol. I, p. 63.

[4] Ad-Damīrī's "Hayāt al-Hayawān" (a zoological lexicon), translated by A. S. G. Jayakar, London, 1906, Vol. I, p. 237.

the remora is found off the coast of Zanzibar, where it is in the same way connected with the catching of large fish. But we have a circumstantial report of the employment of the sucking-fish in the catching of sea turtles in João dos Santos' "Ethiopia oriental," which was published in 1609:

> The fishermen kill turtles at sea [along the coast of Mozambique] in a strange manner. First they catch in certain parts of the sea among the rocks near the coast a kind of fish two spans in length, called by the Moors *sapi*, which is as much the enemy of the turtle as the ferret is of rabbits. The *sapi* has a very dark grey skin inclining to black, and a long thin head ending in a snout similar to that of a pig. Its neck is about half a span long, on the back of which is a shell of the same length and three fingers wide, which is formed of hard and porous furrowed skin with which it clings to the stones as leeches do, and it has the same faculty of sucking blood. For this reason when it meets a turtle it attacks it and wounds it in the neck or legs with this shell, and sucks its blood until it is satiated, leaving the turtle nearly dead, it being unable to resist or get away, as it is large and unwieldy and the *sapi* very nimble.
>
> When the fishermen have caught some of these *sapis* they put them in a basin of salt water and take them in the boat with them. They tie a long line to their tails and then put out to sea in search of turtles, which usually swim on the surface of the water. When they catch sight of a turtle they throw out the fish fastened by the tail, as one lets loose a ferret in a leash after a rabbit, and the fish immediately attacks the turtle with as great force as if it was free and had received no harm from the hook with which it was caught, or as if it was not itself a prisoner. When it reaches the turtle it fastens on it so tightly that it never looses its hold, and as soon as the fishermen feel that it had done so they pull in the line and draw it over the water without its loosening its hold, and the turtle, although very big and heavy, is so dominated and tormented by the fish that it does not fight with it, but lets itself be carried off easily because of the pain it suffers while they are pulling it in, as at that time the fish grips it much tighter. Thus the turtle is brought to the side of the boat, when the fishermen quickly seize it in their hands and lift it in, and the fish they put back into its basin. In this manner they catch a number of turtles.[5]

In the Bantu language of Zanzibar we have "*kassa*, turtle; the *kassa* is caught by means of the *taza* fish,

[5] George McCall Theal, "Records of Southeastern Africa" (London), 1901, Vol. VII, p. 325 ff.

which the fishermen carry alive with them; when they see a *kassa,* they let the *taza* go after it to stick fast to the *kassa*; when the *taza* has seized it, the fisherman throws a harpoon and takes the *kassa* out of the sea, the *taza* letting go instantly when exposed to the air."[6] The same dictionary gives *tasa* "a kind of fish which serves as a bait for turtles,"[7] but the other dictionaries give for it *chazo,* which name is also recorded by Professor Gudger. *Kassa* for "turtle" is of extremely wide distribution and is not primarily a Bantu word, although it is also found as *kasi* in Tete, that is in the region to which dos Santos refers.

The oldest forms on record for this word are Sanskrit *kacchapas, kaçyapas,* Avestan *kasyapa,* hence Persian *keshef,* Afganistan *kasph,* Singhalese *keshew,* Hindustani *kacchua, kaccha.* It is therefore certain that the turtle fishing was brought to the shores of Zanzibar from somewhere in the Indian Ocean. This is in keeping with the frequently recorded tortoise-shell trade in the Indian Ocean, but "opposite the Ganges there is an island in the ocean, the last part of the inhabited world toward the east, under the rising sun itself; it is called Chryse, and it has the best tortoise shell of all the places on the Erythraean Sea."[8] The Chryse Island has been identified with the Malacca peninsula,[9] hence the origin of the practise of catching turtles with the remora is most likely to be referred to the East Indies, whence it traveled eastward, to the Torres Strait and Melanesia, and westward to the eastern shores of Africa.

The earliest definite reference to the remora fishing is contained in a version of the cormorant fishing, as told by Odoric of Pordenone and for the first time printed in Ramusio in 1574, although it can be shown that it was

[6] L. Krapf, "A Dictionary of the Suahili Language," London, 1882, pp. 130 f.

[7] *Ibid.,* p. 362.

[8] W. H. Schoff, "The Periplus of the Erythraean Sea," London, 1912, p. 48.

[9] *Ibid.,* p. 259.

already in existence in the fourteenth century. Odoric of Pordenone told how he came

to a certain great river, and I tarried at a certain city (called Belsa) which hath a bridge across that river. And at the head of the bridge was a hostel in which I was entertained. And mine host, wishing to gratify me, said: "If thou wouldst like to see good fishing, come with me." And so he led me upon the bridge, and I looked and saw in some boats of his that there were certain water-fowl tied upon perches. And these he now tied with a cord round the throat that they might not be able to swallow the fish which they caught. Next he proceeded to put three great baskets into a boat, one at each end and the third in the middle, and then he let the water-fowl loose. Straightway they began to dive into the water, catching great numbers of fish, and ever as they caught them putting them of their own accord into the baskets, so that before long all the three baskets were full. And mine host then took the cord off their necks and let them dive again to catch fish for their own food. And when they had thus fed they returned to their perches and were tied up as before. And some of those fish I had for my dinner.[10]

This is followed by another kind of fishing:

The men this time were in a boat, wherein they had a tub of hot water; and they were naked, and had each of them a bag slung over his shoulder. Now they dived under water (for half a quarter of an hour or so) and caught the fish with their hands, stowing them in those bags that they had. And when they came up again they emptied the bags into the boat, whilst they themselves got into the tub of hot water, and others went in their turn and did as the first; and so great numbers of fish were taken.[11]

The second kind of fishing is interesting from the fact that it was much earlier told by Idrīsī as in use at Zanzibar.

These people (at Meduna) fish in the sea without boats. They fish by swimming, with small nets spun from grass and manufactured by them. They tie these strings to their feet by means of knots which they hold in their hands, they draw the strings of the net together the moment they feel that the fish have entered, and this they do with an art in which they excel, and with rules in which they have long experience.

[10] Sir Henry Yule, "Cathay and the Way thither," London, 1913, Vol. II, pp. 188 ff.

[11] *Ibid.*, pp. 190 f.

To attract the fish they use land reptiles. Although they live in a state of great distress and misery, these people (God loves those who reside at their family hearths) are satisfied with their lots and with what they have. They are under the government of Zanzibar.[12]

Yule[13] cites Fortune and Dabry for the same custom in China, which once more shows the wide distribution of identical maritime customs from Zanzibar to China.

The first kind of fishing has undergone all kinds of changes in the very earliest Odoric manuscripts. Sir John Mandeville, who cribbed so much out of Odoric, tells of a fish-otter, instead of a cormorant, as the animal with which fish are caught.

In that country there be beasts taught of men to go into waters, into rivers and into deep tanks for to take fish; the which beast is but little, and men clepe them *loirs*. And when men cast them into the water, anon they bring up great fishes, as many as men will. And if men will have more, they cast them in again, and they bring up as many as men list to have.[14]

It is interesting and important to observe that the Italian version of Sir John Mandeville which came out in 1491,[15] that is, one year before the discovery of America, has the same story, the French term *loir* for "otter" being here rendered by *udria*. The Latin version, of about 1500,[16] simply says:

Tamed water dogs whom we call *luteres*, are here aplenty; every time they are sent into the river, they bring out fish.

The substitution is everywhere from Vincent of Beauvais, who in his "Speculum naturale," XX, 89, tells of the same fish-otters with which fish are caught, but the substitution is unquestionably older than Sir John Mandeville's, who would not have omitted the strange story of the cormorant if he had found it in his copy of Odoric.

[12] *Op. cit.*, pp. 55 f.

[13] *Op. cit.*, p. 191.

[14] "The Travels of Sir John Mandeville," London, 1900, p. 136.

[15] "Tractato delle piu maravigliose cose e piu notabili," Venice, Nicolaus de Ferrariis, 17 Nov., 1491, cap. CXLVII.

[16] "Johannis de Montevilla Itinerarius in partes Iherosolimitanas," cap. XXXI.

The Latin version of Odoric has the old cormorant story[17] where the bird is called *mergus,* while in the Italian version it is called *smergo.*[18] The usual Italian names for the cormorant which Odoric must have known, are also *mergo, maragone,*[19] so that the Latin *mergus* is formed from the Italian *mergo.* Curiously, there are two versions of Odoric in Ramusio. In the first the whole cormorant fishing episode is omitted, while the second has a totally different account. Here we read:

> Mine host . . . took us to one side of the bridge where the river was wider, and there we found many boats, and there was one of them employed in fishing by aid of a certain fish called *marigione.* The host had another such, and this he took and kept it by a cord attached to a fine collar. And this indeed is a creature that we have seen in our own seas, where many call it the *sea-calf.* It had the muzzle and the neck like a fox's, and the fore paws like a dog's, but the toes longer, and the hind feet like a duck's, and the tail with the rest of the body like a fish's. Mine host made him go in the water, and he began to catch quantities of fish with his mouth, always depositing them in the boat. And I swear that in less than two hours he had filled more than two big baskets.[20]

It is clear that the description of the *sea-calf* is an exaggeration of that of the fish-otter, which is in Arabic called "fox of the water" or "dog of the water." Hence there is most likely here an Arabic influence which caused the substitution. And the reference to a fish *marigione,* which was kept by a cord attached to a fine collar, is similarly an attempt to bring the cormorant story in keeping with the Arabic and Zanzibar account of the fishing with the remora. We have here a transitional stage from the cormorant story to the *remora* story, as fathered by Columbus and permanently incorporated in all later accounts who drew upon the Columbus story.

[17] T. Domenichelli, "Sopra la vita e i viaggi del beato Odorico Da Pordenone," in Prato, 1881, p. 180 (cap. XLVI).

[18] *Ibid.,* p. 232.

[19] Yule, *op. cit.,* p. 352.

[20] *Ibid.,* p. 189.

Professor Gudger has shown, beyond any possibility of cavil, that all the accounts of the remora fishing in America recorded after Oviedo go back to this latter source, and I shall now show that Oviedo's account goes back, through Bernaldez, to an Arabic source, which is itself an evolution of the second Italian version of Odoric's cormorant fishing, as preserved to us in Ramusio.

Bernaldez[21] says: "For they call it hunting, and they hunt one fish with others of a particular kind," while in the "Journal of the Second Voyage"[22] we read: "The fishing consists in this that they take certain fishes which they call *revesos,* the largest of whom are not larger than pilchards," from which Peter Martyr made his "*reversus* fishes."[23] In the Spanish the passage in Bernaldez runs as follows:

> Vino una canoa a casa de pezes que ansí le llamaban ellos *caza,* que *cazan con unos pezes otros.*

It will be observed that all the Columbus accounts tell of the invitation extended by the fishermen to Columbus to see the peculiar kind of fishing, and the giving of the catch to Columbus, according to Bernaldez, for a feast. This is identical with the manner in which Odoric tells of the invitation to watch the cormorant fishing. The resemblance is striking. Now, in the second Italian version in Ramusio the fish with which other fish are caught is called *marigione,* "diver," while others call it *sea-calf.* We have here, side by side, cormorant, otter and remora. I have already shown in my book, "Africa and the Discovery of America," that much of the matter in the "Voyages of Columbus" is apocryphal and comes from Odoric of Pordenone's "Itinerario," a name which Bernaldez uses for the book of Columbus, from which he got his information. There can be little doubt that the sec-

[21] *Loc. cit.,* p. 450.

[22] See my "Africa and the Discovery of America," Philadelphia, 1920, Vol. I, p. 64.

[23] Gudger, *loc. cit.,* p. 297.

ond Italian version was corrected or annotated by Columbus in the margin, where the true story of the remora fishing at Zanzibar was given from an Arabic source, from which Columbus retained two foreign terms. He had found in his source *kassa,* the turtle caught by the remora, and the name was apparently entered into the margin from which Bernaldez got his threefold *caza* "chase." Indeed, it appears that in his "que ansí *le* llamaban ellos *caza," it* referred originally to the fishes caught, that is, to the turtles, which from the resemblance to Spanish *caza,* "chase," produced the unfortunate pun. It will be noticed that in the "Journal of the Second Voyage" the corresponding passage runs "they take certain fishes which they call *reversos,"* where the second Italian version says "fishing by aid of a certain fish called *marigione,"* that is, "diver." Now the Arabic word for "diver" is *gavvāsah.* Anciently the initial guttural was rendered in Spanish by a simple *g,* but in the fifteenth century this Arabic word would sound to a European ear as *reverso* or *reveso,* which it actually assumed in the Columbus story. No such Spanish word is anywhere else recorded for the remora. Again, the marginal gloss, from Bernaldez, "hunting with a fish," must have been "caza con un pez," which Peter Martyr took to be the name of the fish, the remora, hence he misread the first as *guaicanum,* and called this the Indian name for the fish, a word which is only recorded as a quotation from Peter Martyr.

From the previous discussion it follows:

1. The remora fishing is very old and originated in the Indian Ocean, but did not get into literature before Columbus.

2. Odoric of Pordenone's cormorant fishing was from the start confused with the fishing by means of an otter and, in Ramusio's second version, was dimly identified with the remora fishing.

3. Ramusio's second version was, before the time of Columbus, influenced by an Arabic source or explained

by an Arab acquainted with the remora fishing at Zanzibar, and this new form supplied Columbus with the Zanzibar word for "turtle," namely, *kassa,* and the Arabic word for "diver," namely, the Spanish *reves* or *reverso,* which was wrongly attached to the "remora."

4. Bernaldez and Peter Martyr created a non-existing remora story for America out of Odoric's much-revised cormorant story, on the basis of some marginal notes in Columbus's "Itinerario," which itself was based on Odoric's "Itinerario," and referred to Zanzibar and not to America.

5. There are in America no corroborative stories of the remora fishing, except as derived from Oviedo's hearsay account, which itself is based on the accounts of Bernaldez and Peter Martyr, which, in their turn, are taken from a revised edition of Odoric's cormorant fishing story.

SHORTER ARTICLES AND DISCUSSION

REPORT OF THE COMMITTEE ON GENETIC FORM AND NOMENCLATURE

THE American Society of Naturalists at their meeting in 1919 appointed a Committee on Genetic Form and Nomenclature consisting of Drs. S. Wright, G. H. Shull, O. E. White, A. H. Sturtevant and myself as chairman. We were to consider the matter of genetic nomenclature and submit constructive suggestions for standardizing descriptive terms in this subject. "The following report of the committee was submitted to the meeting of the American Naturalists at Chicago, 1920, as a foundation intended to cover the cases of inheritance commonly met with by the majority of experimental workers in genetics. It is submitted in the hope that it may be published to invite discussion as to suggested modifications which would enable it to include particular problems of the scores of investigators in this field. In making such criticisms it is suggested that the primary object of this report be continually borne in mind and that constructive suggestions based on it as a framework are more likely to lead to beneficial results than purely destructive ones. The vast majority of workers in genetics will be concerned with simple enough problems to be covered by the report. Those whose material requires modification of the methods therein suggested will undoubtedly see the justice in attempting to adapt their particular needs to some modification of a system which will meet the needs of the majority."

C. C. LITTLE, *Chairman,*
Committee on Genetic Form and Nomenclature.

In submitting this report your committee desires to call attention to certain matters of general interest in connection with it. It is neither *proposed* nor *supposed* that those now familiar with some characteristic or individual form of genetic nomenclature will necessarily find it desirable to conform with the suggestions contained herein. If they can and will cheerfully do so, so much the better; if not, no intention to dictate is implied in this report.

It is, however, believed that a considerable number of geneticists will agree to the main suggestions of the report, and will thereby form a nucleus to which younger geneticists beginning publication would in a majority of cases join themselves. Thus, after a time, a far more uniform method of publication than now exists would become established.

In order to give such an opportunity, your committee respectfully suggests that this report, if approved by vote of the members present, be published at the earliest convenient time.

1. *The Type.*—In most animals and plants it is convenient to settle on a standard type, preferably the wild type, when this is known. The effects of the various genetic factors are in general to be measured by the departure from type which they bring about. This recommendation involves no real departure from the system now in use by most geneticists.

2. *Series of Allelomorphs.*—A single letter, with a subscript, *if necessary,* is to be assigned to each series of allelomorphs. This letter should, when possible, be chosen so as to give some hint as to the nature of the effects caused by variations in the series in question. The member of each allelomorph series present in the type is to be represented by the symbol for that series, capitalized and with no superscript. Factors dominant over the type are to be represented by the same capitalized symbol as the type, but with appropriate superscripts. Recessives are to be represented by the same symbol in lower case also with appropriate superscripts (*when necessary*). The symbols for the type factors may be omitted in formulæ where convenient. The agouti series in mice A^y, A^1, A, a^n, in which two factors are dominant over the wild gray type and one recessive is an example of the use of symbols. [This series might properly have been given a Y or B symbol in place of the A adopted. Since, however, it is to be thought of in terms of modification of the agouti pattern, the symbol A is chosen.]

3. *Dominance.*—Dominance of genes is recognized to be largely a matter of convenience. Factors may be considered dominant which produce an easily recognized departure from type, when heterozygous.

4. *Superscripts.*—It is suggested that both a literal and a numerical superscript be assigned, *upon the initial description,* to each factor except the type (at least in series of multiple allelomorphs). EITHER SUPERSCRIPT MAY THEREAFTER BE USED ALONE. The numerical superscript shall indicate the estimated

degree of divergence from type, produced by the factor in question in a scale in which 10 is the apparent physiological or visible limit and 0 is the type. Thus A^{10} and a^{10} represent factors which cause deviations to the physiological limit in opposite directions (self yellow and self black) from the type A (agouti). A^4 (light-bellied agouti) represents an estimated deviation between ticked bellied agouti (A) and yellow (A^{10}). *The order of effect is more important than a precise estimate of the degree of effect.* Decimals and numbers beyond 10 may be used whenever necessary, in event of grades not believed physiologically possible. A superscript, once adopted, should not be changed, which also applies to all other symbols. The value of making provision for a system to *indicate the order* of a multiple allelomorph series is clear; the numerical symbols will only be *used* when such a situation is encountered.

5. *Independent Factors.*—Independent series of allelomorphs should be represented by different letters or, if desired, by the same letter with different following numbers. Symbols composed of two or more letters should not be used. It is suggested that factors with more or less similar effects be represented by the same letter with different following numbers, as S1, S2, S3, etc. The same symbol may conveniently be used for factors with more or less similar effects in different animals and plants without implying identity.

6. *Doubtful Factors.*—In case the formula of an individual is not fully known, the uncertain factor may, if desired, be represented by a superscript X (or ?) or the whole symbol may be replaced by a dash. Thus C^x C^x (or $C^?$ $C^?$) means *complete* ignorance of the factor in series C. CC^x, $CC^?$, or C — represents ignorance as to one of the factors in the zygote. If there is partial knowledge, a double (or triple) superscript may be used to indicate the various possibilities. Thus the progeny of the cross CC × c^rc^a may be represented by C c^{ra}, a form which gives more information than C —.

7. *Modifiers.*—The symbol [ ] containing appropriate symbols represents residual heredity of the kind indicated. Thus [S +] is a convenient method of representative + modifiers of the effect produced by the S (Spotting) series of allelomorphs. In a detailed study of a particular group of modifiers, the parenthesis may well contain the grade of effect produced by the modifiers in the case in question. Thus [+ 4.2] and [—2.5] might be used to represent the modifiers of typical hooded rats of grades

+4.2 and —2.5. The modifiers of a cross bred may be indicated in some appropriate manner as [+4.2, —2.5].

8. *Linkage* is best represented by the fractional form used by workers on *Drosophila*. The factors are written in the order of linkage, omitting type factors.

COMMITTEE ON GENETIC FORM AND NOMENCLATURE

STANDARDIZED MICROPHOTOGRAPHY

SECOND CONTRIBUTION: THE OBJECT FACTOR

IN my first contribution to the subject of standardized microphotography, published in the *Anatomical Record*, I have pointed out the variables and the methods which I have pursued in treating them. One, or perhaps more correctly a group of variables were, however, left out of consideration quite purposely because of the difficulty in finding for them a standard of permanent value. I have in mind the microscopical section itself or what may be properly called the object factor. The following four elements enter into its composition: (1) the thickness of the section, (2) the light absorption coefficient of the tissue, (3) the relative luminosity of the different stains and (4) the depth or intensity of staining. The second and third of these component elements may be disregarded since experience shows us that exposure is very little influenced by them. There remain, however, the first and fourth, and to determine the influence of these on exposure the following experiments were undertaken.

First of all, to avoid all possible error, slides were chosen of uniform thickness measured with a Ciceri Smiths Patent Micrometer so as to be sure that the distance of the section from the substage condenser should in every case be the same. The cover-glasses were also of uniform thickness. The stomach of a frog preserved in Zenker's fixing fluid was sectioned into series of 5, 10 and 20 micromillimeter thick sections on a Minot microtome and care was taken to have in each case a ribbon of 100 even sections, thus more or less assuring their uniform thickness. The sections were stretched on distilled water heated over a flame and no cement of any kind was used. On one slide three sections of each thickness were placed. On other slides sections only of one kind were placed and their thickness marked in every case by a carborundum pencil.

The slide with all three kinds of sections was stained for 12 hours in alumcarmine, a stain which, as is well known, does not overstain. They were then washed in water and again stained for 12 hours in a weak alcoholic solution of Bleu de Lyon. All sections on this slide received therefore the same treatment and the difference in the depth of stain was entirely due to the thickness of the section stained.

The other slides were treated in a different way. They were stained in Delafield's hæmatoxylin followed by tetrabromfluorescic acid. This stain was chosen because it is possible at will to control the depth of staining. A set A of three slides, one with 5 micromillimeter sections, one with 10 and one with 20, was treated simultaneously in a Coplin's staining jar. The sections were therefore stained, washed, destained in acid alcohol, treated with ammonia alcohol, stained in a weak solution of tetrabromfluorescic acid in 95 per cent. alcohol and washed in pure alcohol the same length of time. In regard to depth of stain these slides presented, therefore, the same conditions as the slide stained in alumcarmine and Bleu de Lyon.

Several other slides were treated individually in the same stains. They were all first considerably overstained in Delafield's hæmatoxylin, washed in water and destained in acid alcohol until they had when viewed over a white surface, the same shade of color to the naked eye, regardless of the thickness of the section. If after treatment with ammonia alcohol the blue color was not approximately of the same shade, the darker slide was again transferred to the acid alcohol, until all sections looked approximately alike. They were now stained in the tetrabromfluorescic acid, the thickest sections remaining a short time in the fluid, the 10 micromillimeter sections somewhat longer and the 5 micromillimeter sections longest, and again compared over a white surface. From several slides thus prepared three were selected which to the naked eye were to all purposes of the same appearance, although their respective thickness were 5, 10 and 20 micromillimeters. Here then we had a Set B of sections in which the depth of stain had nothing to do with the thickness of the section, but was entirely dependent upon the amount of stain absorbed by the tissues.

Fractional exposures on orthonon plates with Cramer ray-filters were made on our standardized microphotographic apparatus and developed by the time and temperature method with

fresh developer for each plate. In the case of the first slide stained in alumcarmine and Bleu de Lyon as in the Set A, the normal exposure for the 10 micromillimeter section was twice that for the 5 one, and the normal exposure for the 20 micromillimeter section was four times that of the 5 one. In the case of the Set B all slides required the same exposure.

In analyzing the results thus obtained we come to the conclusion that the thickness of the section, within the limits given, has no influence whatsoever on the length of exposure; but that the latter stands in a direct ratio to the amount of stain absorbed by the tissue.

For practical purposes, especially for those who are using my table of R-P factors, the results of this investigation may be interpreted as follows: disregard the thickness of the sections and the appearance of the stain under microscope and pay attention only to the intensity as it appears to the naked eye. The table refers to normally well stained sections of medium thickness. Double the exposure for darker appearing and reduce the exposure by half for lighter appearing sections.

It will be observed that in the experiments elements 2 and 3 remained of constant value for the simple reason that the tissue used was not only the same in kind, but actually from the same piece of organ and was stained in the same stain in each set of slides. A comparison of the length of normal exposure in the case of sections stained in alumcarmine and Bleu de Lyon with those stained in hæmatoxylin and tetrabromfluorescic acid serves to confirm my statement at the beginning of this article, that the relative luminosity of different stains may be entirely disregarded in the matter of exposure.

ALEXANDER PETRUNKEVITCH

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SEX RATIOS IN PLATYGASTER

IN the *Journal of Heredity* for last year (Vol. X, p. 344) I published data on sex ratios in three species of polyembryonic Hymenoptera. One of these is *Platygaster felti,* which parasitizes the eggs of two species of the Cecidomyiidæ, *Walshomyia taxana* and *Rhopalomyia sabinæ.* These flies make their galls on the mountain cedar, *Sabina sabinodes.*

Since the above data were published I have had an opportunity to breed out in the laboratory a total of 200 broods of

Platygaster; 73 from the carcasses of *Rhopalomyia* and 128 from those of *Walshomyia.* The remarkable character of the sex ratios, as revealed in the published data, is emphasized by the additional facts secured from the more recent rearings. It therefore seems worth while to publish the full data, which is given in condensed form in the following table. In the first column the total number of individuals in each brood is given; in the second, the number of females; and in the third, the number of males. In the fourth column are listed the number of broods showing the combination of females and males in the corresponding horizontal line.

The total number of individuals in the 200 broods is 2,722, of which 2,346 are females and 376 males. The average per brood is 13.61. The size of the brood reared from *Walshomyia* is very much smaller than those from *Rhopalomyia.* There are 1,417 individuals in the 128 broods from *Walshomyia,* or an average of 11.07 per brood. The broods from *Rhopalomyia* have 1,305 individuals, or an average of 18.12 per brood. This represents an average increase of 63.6 per cent. The rate of increase in the number of males per brood from *Walshomyia* to *Rhopalomyia* is almost the same as this. The average number of males in broods from *Walshomyia* is 1.55, and in those from *Rhopalomyia* is 2.45. This represents an increase of 58 per cent.

The difference in the size of broods is, in all probability, due to the difference in the size of the two host larvæ. The larva of *Rhopalomyia* is almost twice as large as that of *Walshomyia,* and hence must furnish a more abundant food supply for the multiplication of embryos at the time of their formation in the polygerm.

One of the most striking facts in the data is the preponderances of females. Approximately 86 per cent. of the individuals are females. No male brood has been found, and in not a single instance does the number of males exceed or even equal the number of females in a brood. There are, however, nine pure female broods. Of the 191 mixed broods 113, or 59.61 per cent., have a single male present in each brood. The other 78 broods show the following numbers of males: Thirty with two males each; twenty-four with three each; ten with four each; four with five each; four with six each; three with seven each; two with eight each; and one with ten.

Another interesting fact is the frequent occurrence of broods with a single male. Almost sixty per cent. of the mixed broods

TABLE I

BROODS OF PLATYGASTER FELTI

No. of Individuals	Females	Males	No. of Broods
5	3	2	1
5	4	1	1
6	5	1	4
7	5	2	1
7	6	1	14
8	6	2	2
8	7	1	9
9	7	2	2
9	8	1	13
9	9	0	3
10	7	3	1
10	8	2	1
10	9	1	31
10	10	0	1
11	8	3	2
11	9	2	4
11	10	1	15
12	10	2	2
12	11	1	3
13	9	4	1
13	10	3	3
13	11	2	3
13	12	1	5
13	13	0	1
14	10	4	1
14	11	3	2
14	12	2	2
14	14	0	1
15	12	3	1
15	13	2	6
15	14	1	7
15	15	0	1
16	13	3	2
16	14	2	2
16	15	1	3
16	16	0	1
17	13	4	1
17	14	3	2
17	15	2	2
17	16	1	2
18	14	4	1
18	15	3	2
18	17	1	4
19	15	4	1
19	16	3	3
19	17	2	1
19	19	0	1
20	16	4	1
20	17	3	1
21	17	4	1
21	18	3	1
22	17	5	2
22	20	2	1
22	21	1	2
23	19	4	1
23	20	3	2
24	20	4	1
25	17	8	1

TABLE I (*Continued*)

BROODS OF PLATYGASTER FELTI

No. of Individuals	Females	Males	No. of Broods
26	20	6	1
26	21	5	1
26	22	4	1
26	23	3	1
27	21	6	1
28	25	3	1
29	24	5	1
31	24	7	2
34	26	8	1
34	27	7	1
36	26	10	1
36	30	6	1
37	31	6	1

are of this character. Certain combinations, such as nine females and one male, occur with very great frequency, suggesting that a single male is produced at some definite point in development. Statistical treatment of the data supports this suggestion. My colleague, Dr. Muller, has kindly calculated the standard error and standard deviation of the numbers of males per brood, and finds that they are 1.17 and .64 respectively. These results show that the number of males produced per brood does not vary as much as it would if males were formed at random. If males were produced at random, the amount of variation in the number of males would be expressed by a standard deviation of 1.17. This means that there is a tendency to have the production of males confined to particular cells in the embryonic mass, so that only one or two males are usually formed in a brood.

The fact that the parasite deposits one egg at each oviposition makes it practically certain that the mixed brood of *Platygaster* is the product of a single fertilized egg. The important question is how the single male originates during the course of development. I have elsewhere discussed this question, and have suggested that the appearance of one or more males in a brood may be due to an abnormal behavior of the sex chromosomes. An abnormal division causing the loss of an x-chromosome from one of the early blastomeres would explain the appearance of a mixed brood, for such a cell could become the progenitor of one or more males.

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REPRODUCING POWER OF WELL-FILLED VS. POORLY-FILLED EARS OF MAIZE

THESE tests were conducted to determine the effects, if any, on the progeny, particularly as to productivity, when a stalk of corn is caused to produce comparatively few kernels instead of a normal-sized, well-filled ear. In other words, the object was to learn whether artificially reducing the possible number of progeny kernels would have any influence on their viability, vigor or ability to yield.

In selecting seed corn, ears are occasionally found which evidently would have been much larger and better filled had not something such as an overhanging blade or an insect interfered with pollination. Are such ears suitable for seed?

Similar tests were conducted with three varieties, one being a cross-bred variety. The three classes of seed for these tests were grown in 1914 and their comparative productiveness tested in 1915. The seed of U. S. Selection 77 was grown and tested at Piketon on river-bottom soil in Southern Ohio, and that of the other two varieties at Broad Run on Piedmont clay of Northern Virginia.

METHODS OF PROCEDURE

Two methods were used to control the pollination and consequent seed production of the poorly filled ears. In one case, the first silks to appear were about an inch beyond the end of the shoots when the shoots were bagged to prevent further pollination. In the other case, the ear shoots were bagged before the silks began to appear. When all the silks had protruded several inches the bags were removed for half an hour and then replaced. This was done when pollen was falling freely. A few of the uncovered silks thus became naturally pollinated.

The first method produced ears the butt ends of which were fairly well filled for about one fourth the length of the cob. The second method gave ears that had a few large rounded kernels scattered over the cob. As check seed for the tests, large, well-filled, typical, seed ears that had been allowed to mature unmolested were selected. The seed ears of the three lots of each variety were selected from the same rows from similar stalks grown under like conditions as far as possible. The drying, care, etc., were the same for each of the three lots.

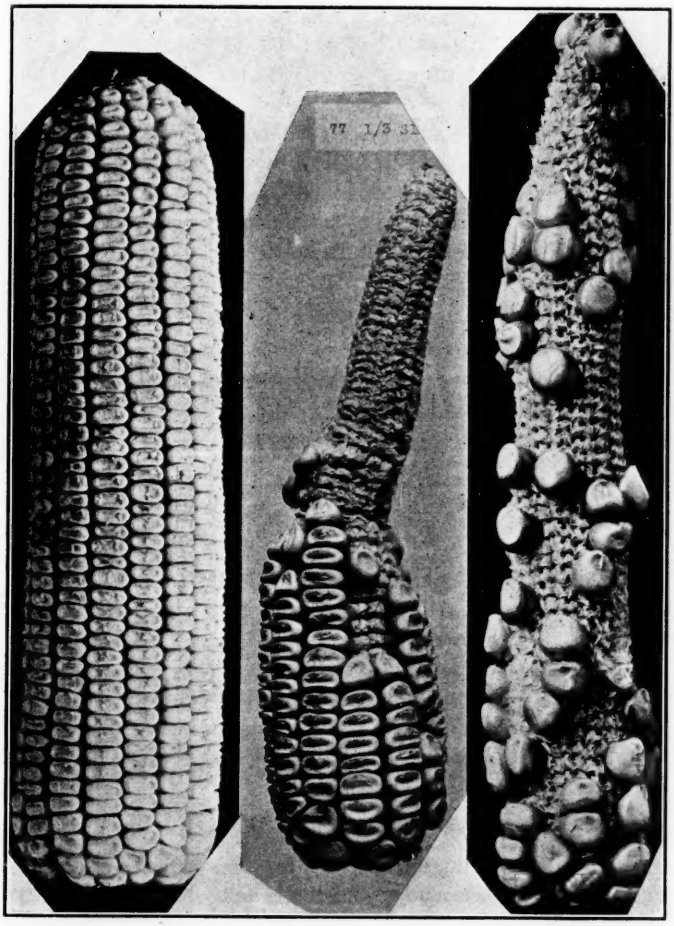

FIG. 1. Comparative productivity tests were conducted with lots of seed taken from the three kinds of ears here represented.

The seed from the check ears will be referred to as such while that from the ears filled only at the butt ends, as Lot 2, and that from the ears with kernels scattered over the cob as Lot 3.

The number of ears used in making up each lot of seed follows: Selection 77, Check, 62 ears; Lot 2, 67 ears; Lot 3, 54 ears; Selection 119, Check, 26 ears; Lot 2, 19 ears; Lot 3, 26 ears; and Cross 182, Check, 26 ears; Lot 2, 14 ears; and Lot 3, 19 ears.

In preparing for planting each lot was composited in the following manner. The same number of kernels was taken from each ear of a lot and these kernels combined made just enough to plant one row 50 hills long. The comparative weights of the three lots of seed are given in Table I.

TABLE I

WEIGHTS IN GRAMS OF 265 KERNELS OF EACH LOT OF SEED

Variety	Check Seed	Lot 2	Lot 3
Selection 77	124	141	137
Selection 119	118	122	127
Cross 182	126	148	151

DATE AND METHOD OF PLANTING

U. S. Selection 77 was planted May 1, 1915. The three lots were planted in adjacent rows and the test repeated 14 times. Selection 119 and Cross 182 were planted May 3, 1915. The lots of these two varieties were planted in the same order as the lots of Selection 77, but only 15 rows each of these two varieties were planted. The planting was done by hand and later all the rows were thinned to a uniform stand.

OBSERVATIONS DURING GROWTH

At no stage during the growth of the corn was there any noticeable difference among the three lots. Neither was there any difference in the time of silking and tasseling, in the height of stalk, nor in time of maturing. There was a slight difference in the field germination of the three lots of seed as shown in Table II., but these differences within the varieties are not great enough to be significant nor are they consistent for the three varieties.

TABLE II

Variety	Lot	Field Germination, Per Cent.	Ave. Weight of the Ears Produced, Pounds	Total No. of Stalks	Total Yield of Ears, Pounds	Corrected Yield per Acre, Bushels
Selection 77.....	Check	87.6	0.763	1,725	1,292.0	96.7
	2	86.6	0.736	1,738	1,228.0	89.9
	3	86.6	0.761	1,723	1,277.0	94.5
Selection 119....	Check	84.5	0.592	481	308.1	74.8
	2	84.5	0.586	472	283.1	70.9
	3	79.7	0.585	494	290.6	69.7
Cross 182.....	Check	83.8	0.682	503	346.4	80.1
	2	88.3	0.635	507	321.2	74.8
	3	80.8	0.662	510	331.4	77.0

RESULTS

The yields in Table II. are all based on field weights at harvest time. With all three varieties the well-filled seed ears produced the highest yields, the increase being from 2.2 to 3.9 bushels per acre over the next highest lot. In the 25 comparisons between the two lots, Checks outyielded Lot 3, its nearest competitor, 16 times, with one tie; and it outyielded Lots 2, 20 times with two ties.

Previous work had proved Cross 182 more productive than Selection 119. In the tests reported in Table II. they occupied the same amount and kind of soil and Cross 182 is consistently more productive than Selection 119.

Regarding all three varieties the ears harvested from each of the three lots of seed were equally well-filled and of the same general appearance. These tests warrant the conclusions that ears poorly-filled by reason of withheld pollen will not transmit this character to their progeny, and can be expected to supply seed almost as productive, if not as productive, as they would have supplied if completely pollinated.

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ANTHEROPHAGUS OCHRACEUS MELS. IN THE NESTS OF BUMBLEBEES

THE recent appearance of two articles on "The Phoresy of *Antherophagus,*" one by W. M. Wheeler (1919) and the other by H. Donisthorpe (1920) have prompted me to publish some additional observations on the habits of *Antherophagus ochraceus* Mels. in this country.

Wheeler writing in December, 1919, recorded the capture of an adult of this beetle near Colebrook, Connecticut, attached to the proboscis of a worker bumblebee (*B. vagans*). When the bumblebee, which vainly tried to rid herself of the beetle, was placed in a cyanide jar, the beetle still maintained its hold. In this same article there is a discussion of the phenomenon of "phoresy" as defined by Lesne (1896) and expanded by Janet (1897), together with an account of the known habits of *Antherophagus* and a bibliography. Donisthorpe in October, 1920, published a résumé of Wheeler's paper, presenting further information concerning "phoresy" in general, the habits of *Antherophagus,* and additional references. Scott (1920) has also contributed to our knowledge of the biology of these beetles.

Many of the rather numerous European references report the finding of *Antherophagus* (*pallens, silaceus* and *nigricornis*) and of *Cryptophagus* (*setulosus,* and *sp.*) in the nests of various species of bumblebees. The only American record actually citing an instance of finding *Antherophagus ochraceus* Mels. in the nests of bumblebees is that given by A. S. Packard (1864) based on observations made by F. W. Putnam in Massachusetts and Vermont. J. B. Smith (1909), without giving any data, says that *Antherophagus* occurs in the nests of bumblebees. This latter note is probably based on the statements by Packard, or else on accounts of the habits of the European members of this genus.

While in Wisconsin last summer (1920), I was able to examine many bumblebees nests in various parts of that state, through the kindness of Dr. S. B. Fracker. On two different occasions I found *Antherophagus ochraceus* (C. A. Frost det.) in the nests. In one nest of *Bremus* (*Bombus*) *fervidus* (Fabr.) examined August 12, 1920, were eighteen adult specimens of this beetle.

At the same time and place I took thirty-four larvæ of a small beetle in various stages of development. As these larvæ were associated with the beetles and as they agree with the figure and brief description of *A. ochraceus* given by Packard (1883), I assume them to be the same. In another nest of *Bremus* (*Bombias*) *auricomus* (Robt.) opened on July 26, 1920, at Clyman Junction, Wisconsin, I found a single adult of *A. ochraceus.* Again on October 3, 1920, near White Heath, Illinois, I collected about a dozen small beetle larvæ in a surface nest of *B. Pennsylvanicus* (DeGeer). These last-mentioned larvæ differ slightly from those found in the nest at Baraboo, Wisconsin, and if not the same species may represent another species of *Antherophagus.*

There has been much discussion as to the feeding habits of the adult and larval *Antherophagus.* Wheeler, after a survey of the literature of the subject, came to the conclusion that the larvæ were "in all probability merely scavengers in the *Bombus* nests." Wagner (1907) expresses the idea that they "will occasion enormous destruction in the nest," but without giving an instance of the same. I believe that these insects are purely scavengers, not only feeding on the excrement of the bumblebees as suggested by some, but also on all kinds of refuse as maintained by Reuter (1913). In the nests I examined containing *Antherophagus ochraceus,* the beetles and larvæ were never on that portion of the comb then being used by the bees. They were always either on the old decaying empty cocoons on the bottom of the nest, or in the débris directly beneath or surrounding the comb. Such are not the habits of the true parasites and harmful inquilines of bumblebees. The larvæ of *Vitula* (*Nephopteryx* in litt.) *edmansii* described by Packard from the nests of bumblebees feed on the pollen, honey, wax or cells of the comb. To escape being killed by the bumblebees or carried out of the nest, the larvæ of this moth spin a regular labyrinth of silken tubes or cases and never expose themselves to the bumblebees. The larvæ of *Antherophagus* do not spin protective cases and are in no sense of the word parasitic on the adult bees, larvæ or pupæ. If they, thus unprotected, should crawl conspicuously over the comb to destroy the eggs, larvæ or pupæ, or to eat the new comb and stored food, they could easily be combated by the bumblebees. Furthermore, the nest containing the thirty-four larvæ and eighteen adult beetles taken at Baraboo, Wisconsin, showed no signs of the great destruction mentioned by Wagner. For that time of

year, August 12, it was in fact a strong colony, containing ninety-one workers, fifty-six pupal cocoons, and large stores of honey and pollen. It is possible that the upper part of the comb of a bumblebee nest might develop so swiftly in some cases, as to cause some cells either filled or not filled with pollen and honey on the lower part of the comb to be neglected, and thus infested with *Antherophagus*. This last statement, however, would certainly be the exception rather than the rule. In the cases that have come under my observation *A. ochraceus* played the rôle of a scavenger, in the débris beneath and about the nest, feeding on the refuse comb, feces, honey, or bits of pollen and wax that perchance had fallen to the bottom of the nest.

Wheeler voices the opinion of Sharp (1899) that the instincts of the beetle permit it to recognize the bumblebee, but not to enable it to find the nest. Therefore the beetle waits on flowers until it can attach itself to a bumblebee and be conveyed to the nest of the latter. Donisthorpe suggests that "it is not so much that they [*Antherophagus*] lack the instinct to find the bee's nest, but rather that it gives them protection from their hosts when they arrive there." *Antherophagus* may or may not be able to find the nests of bumblebees of its own accord, but I am inclined to doubt whether the occasion of the "phoresy" is protective, in that it gives "them protection from their hosts when they arrive there," by their having acquired the nest "aura." If *Antherophagus* is a scavenger, as the evidence seems to indicate, and keeps well hidden in the débris on the bottom or sides of the comb, why is there a need for a nest "aura"? One of these beetles carried to a bumblebee's nest, in all probability, soon after arriving there, releases its hold and falls down to the lower part or bottom of the nest. Many other beetles are accidental visitors or inhabitants of such nests, and living thus in the material about and beneath the comb are not noticed by the ever-watchful bees and go unmolested. W. H. Tuck (1896, 1897) lists over sixty species of beetles from the nests of various species of bumblebees in England, most of which are undoubtedly only casual intruders. I have taken specimens of *Harpalus* sp. and *Onthophagus hecate* Panz. in the nests of bumblebees. Such beetles are much larger than *Antherophagus*, are not even considered as "anthophilous" (Lovell, 1915), nor have they ever been accredited with habits of "phoresy." Evidently then, such beetles gain entrance to the nest and live there for a time at

least without having first acquired a nest "aura." I believe that *Antherophagus* often, if not always, forces the bee to carry it simply in order to find the nest, and not to acquire a nest "aura," such as all the bees of each and every colony possess. If *Antherophagus* had habits similar to those of the inquiline-bee *Psithyrus*, there would be an advantage in having a nest "aura."

Scott (1920) says that

> Presumably these [*A. pallens*] beetles are double-brooded, with a short summer generation intervening between the emergence of the adults in May and the assumption of the resting condition by the larvæ in autumn.

I have taken adults of *A. ochraceus* by sweeping flowers on May 7 and 23, 1917. The insect collections of the Illinois State Natural History Survey contain adults taken on July 19, 23 and 30, 1891, and August 15, 1893. Blatchley (1910) mentions the species as occurring on flowers, June 24 to September 21. As previously mentioned I took one adult in a bumblebee nest on July 26 and eighteen more on August 12. The adults taken on May 7 and 23 certainly represent the hibernating brood. Those found both out of doors and also in a nest on July 19–30, are in all probability the adults of the first brood or summer generation. Those taken on August 12–15, may represent a true second summer generation, but more than likely belong to the same brood of July 19–30. Scott found that *A. pallens* hibernated as larvæ, pupating in early summer. Some of the larvæ presumably those of *Antherophagus* which I took on October 3, when examined on November 11, 1920, had constructed cells in the earth on the bottom of the rearing jar; thus indicating that they hibernated as larvæ. Summarizing these records: *A. ochraceus* is probably double-brooded, hibernating as larvæ in cells in the soil or material about or under the bumblebee nest.

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